EFFECTS OF LOSS AVERSION ON THE EVALUATION OF DECISION OUTCOMES

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Aikaterini Kokmotou.

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List of Abbreviations

ACC	Anterior cingulate cortex
ANOVA	Analysis of variance
BOLD	Blood oxygenation level dependent
dACC	Dorsal anterior cingulate cortex
DLPFC	Dorsolateral prefrontal cortex
ECD	Equivalent current dipole
ECG	Electrocardiographic
EEG	Electroencephalography
EOG	Electrooculographic
ERN	Error-related negativity
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
FRN	Feedback-related negativity
OFC	Orbitofrontal cortex
PCC	Posterior cingulate cortex
PET	Positron emission tomography
PFC	Prefrontal cortex
PT	Prospect theory
rACC	Rostral anterior cingulate cortex
SCR	Skin conductance response
SD	Standard deviation
SEM	Standard error of mean
VLPFC	Ventrolateral prefrontal cortex
VMPFC	Ventromedial prefrontal cortex
VS	Ventral striatum
WTA	Willingness to accept
WTP	Willingness to pay

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This thesis is submitted in fulfilment of the conditions for a PhD by published papers. In accordance with the University of Liverpool guidelines and regulations the experimental Chapters (Chapters 3 to 6) of this thesis will take the form of journal article manuscripts, which have either been published during the preparation of this thesis, are under review in a peer-reviewed journal, or are being read by co-authors before submission to a peer-reviewed journal. Specific details with regards to journal submission are given at the beginning of each Chapter.

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Effects of loss aversion on the evaluation of decision outcomes

Aikaterini Kokmotou

Abstract

Loss aversion is the tendency to prefer avoiding losses over acquiring gains of the same amount. This thesis aimed to explore the neural correlates of loss aversion and its effects on the evaluation of monetary decision outcomes. Decision making in different contexts was investigated in order to identify specific conditions that could modulate the loss aversion effects.

Individual differences in loss aversion were estimated by employing a gambling task and parametric modelling of participants' choice behaviour. Electroencephalographic (EEG) recordings and event-related potential (ERP) analysis were utilised in order to investigate the neural mechanisms underlying loss aversion during the processing of decision outcomes.

Results from across four experimental studies showed that loss aversion was consistently associated with feedback ERPs. Specifically, the first study demonstrated that loss aversion was associated with feedback-related negativity (FRN) component after learning the decision outcome. Individual differences in orbitofrontal cortex (OFC) activity during the FRN time window were further associated with individual differences in loss aversion. In the second study, loss aversion was associated with FRN as well as with P300 component following obtained gains and losses. However, no such associations were found for counterfactual gains and losses (i.e., outcomes that could have been obtained if a different decision has been made). The third study showed that outcomes from choices made by participants themselves and outcomes resulting from choices that were arbitrarily inflicted upon participants were processed differently. This effect was specific for losses in that losses resulting from unchosen decisions produced stronger ERP amplitudes compared to losses resulting from decisions chosen by participants. Furthermore, this result was only found for participants who displayed increased P300 amplitudes following an obstruction of their choice and loss aversion was associated with FRN only in the condition of outcomes freely chosen by those participants. The fourth study investigated loss aversion within a social context and revealed that participants experienced similar levels of loss aversion for themselves and others. For decisions regarding the self, the classic FRN was found, however, for decisions regarding others, the FRN was of opposite polarity. Furthermore, loss aversion was associated only with FRN following decisions that participants made for themselves but not with FRN following decisions that participants made for others.

This thesis concludes that individual differences in loss aversion exert robust effects on the neural evaluation of decision outcomes. These effects were represented in feedback ERP components, under the condition that decision outcomes had real monetary consequences for the decision makers. Moreover, specific conditions that could modify the association between loss aversion and feedback ERPs were identified. The motivational significance of the decision outcomes for the decision makers appears to be the main factor shaping such effects.

Chapter 1

General Introduction

1.1 Decision making, loss aversion and outcome processing

Decision making affects nearly all aspects of daily life. Understanding how individuals make choices and how the brain evaluates alternative prospects has implications for improving everyday decision making (Camerer et al., 2005; Rustichini, 2009). Both environmental and idiosyncratic factors can interfere with the decision maker's ability to make optimal choices (Camerer and Hare, 2013; Glimcher, 2004), and this is even more problematic in cases where such factors are subliminal (Pessiglione et al., 2008). Importantly, many decisions involve risk, which is often associated with potential negative consequences (Platt and Huettel, 2008).

In this thesis, decision making was investigated within the framework of prospect theory (PT; Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), one of the most influential models of choice behaviour (Fox and Poldrack, 2013; Trepel et al., 2005). Specifically, the research that will be described in the following sections investigated the neural mechanisms of loss aversion, which is a core component of PT. Loss aversion refers to the notion that decision makers tend to prefer avoiding losses over acquiring gains of equivalent size (Kahneman and Tversky, 1979). Although extensive behavioural research has highlighted the influence of loss aversion on economic choice (Camerer, 2005; Novemsky and Kahneman, 2005), its neural underpinnings are still poorly understood (Fox and Poldrack, 2013).

After a decision has been made, its outcomes need to be evaluated by the decision maker in order to determine whether the decision led to a desirable consequence or whether the course of the decision making process needs to be changed in order to produce better future results (Rangel et al., 2008). Neuroimaging research has demonstrated where and when this outcome processing occurs in the brain (for reviews see Bartra et al., 2013; Glimcher, 2013), although several questions still remain unanswered, especially regarding risky and uncertain choices (Tobler and

Weber, 2013). Understanding the neural mechanisms that underlie decision making and the factors that can influence choice is important both from a theoretical point of view and for improving actual decision making (Camerer et al., 2005). Furthermore, knowledge of the brain's function, and therefore dysfunction, has implications for understanding maladaptive decision making. For example, several psychiatric disorders are characterised by impairments in decision making and altered hedonic evaluation of choice outcomes, such as heightened sensitivity to negative emotions and events (Endrass et al., 2013; Horan et al., 2012; Nieuwenhuis et al., 2005b; Trémeau et al., 2008). Therefore, detailed knowledge about the neural processing behind decision making and its associated impact on behaviour might provide helpful insights into particular decision making deficits, which could be targeted by specific interventions.

1.2 Prospect theory

Early economic theory (reviewed in Trepel et al. (2005)), was based on the assumption that decision makers choose the option that is associated with the highest expected value (EV). A simple example is a prospect that offers a specified amount of money x with probability p and nothing otherwise. In such a case, the EV of the prospect is calculated by multiplying the amount of money with its associated probability, so that $EV = p \cdot x$. Therefore, a decision maker should always prefer a risky prospect that offers a 50% chance of a £100 gain over a sure gain of £49, because the EV of the gamble is higher than the value of the sure option. However, EV maximisation does not account for risk aversion, as, for example, in the case that the decision maker preferred the sure gain over the risky prospect.

To account for this, Bernoulli (1954/1738), cited in Trepel et al. (2005), proposed that decision makers do not evaluate prospects by their objective EV but rather by their subjective utility, and that the utility of a given amount of money decreases as wealth increases. This diminishing sensitivity gives rise to a utility function that is concave over levels of wealth. A concave utility function means that the utility of £50 is more than half the utility of £100, so that a decision maker should prefer receiving £50 for sure over a 50% chance of receiving £100.

A set of axioms have been proposed by von Neumann and Morgenstern (1947), cited in Fox and Poldrack (2013), in order to formally represent a decision maker's choices by the maximisation of expected utility. One of the central axioms of expected utility theory (EUT) is the 'substitution' or 'independence' axiom, according to which if a decision maker prefers prospect A over prospect B then this preference should not be influenced if prospects A and B are combined in a third prospect. Another central EUT axiom is the 'sure-thing' principle (Savage, 1954), according to which if two options yield the same consequence when a particular event occurs, then a decision maker's preference between these options should not depend on the particular consequence that they have in common.

However, Allais (1953), cited in Kahneman and Tversky (1979), questioned both of the above axioms by designing a range of decision questions that are referred to as the Allais paradox (Allais, 1953, 1979). The following version was adapted from Kahneman and Tversky (1979):

Decision A: 80% chance of £4000 gain (1) or 100% of £3000 gain (2).

Decision B: 20% chance of £4000 gain (3) or 25% of £3000 gain (4).

Most respondents choose (2) over (1), but (3) over (4). However, choices (3) and (4) are ¼ of choices (1) and (2), respectively. As such, the above responses violate the substitution axiom, according to which (3) should be preferred over (4) if and only if (1) is preferred over (2).

Decision C: 33% chance of £2500 gain, 66% chance of £2400, 1% chance of £0 (5) or 100% chance of £2400 gain (6).

Decision D: 33% chance of £2500 gain (7) or 34% chance of £2400 gain (8).

In this case, most respondents prefer (6) over (5), but (7) over (8). However, choices (5) and (6) can be transformed into choices (7) and (8), respectively, by eliminating their common consequence (i.e., 66% chance of £2400 gain). As such, the above responses violate the independence axiom, according to which (7) should be preferred over (8) if and only if (5) is preferred over (6).

PT is a decision making model that explains choice behaviour under risk (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992). It was developed as

an effort to explain the inconsistencies with EUT described in the previous paragraphs and to account for the observation that decision makers do not always behave as completely rational agents (Kahneman and Tversky, 1979).

According to PT, the value V of a simple prospect that offers *x* with probability *p* and nothing otherwise is given by:

$$V(x, p) = w(p) \cdot v(x),$$

where *w* measures the impact of probability *p* on the attractiveness of the prospect, and *v* measures the subjective value of outcome *x*.

Specifically, PT describes decision making under risk between prospects with known probabilities, and can be described by two functions, the value function and the probability weighting function (Kahneman and Tversky, 1979).

1.2.1 Value function

PT assumes an S-shaped value function, which is depicted in Figure 1.1. The value function has three properties. Firstly, the value function measures the subjective value of gains and losses relative to a reference point (Kahneman and Tversky, 1979). This reference-dependence property of the value function means that decision makers evaluate outcomes as positive or negative (e.g., amount of money won or lost) relative to a given reference point rather than from absolute levels of wealth. For monetary outcomes, a zero reference point or the status quo (wealth level at the time of the decision) generally serve as the reference point distinguishing losses from gains. In this framework, a decision maker perceives any negative departure from zero or from the status quo as a loss, while perceives any positive departure as a gain.

Secondly, the value function has a shape that is concave for gains and convex for losses (Abdellaoui, 2000; 2007; Gonzalez and Wu, 1999). The curvature of the value function implies risk aversion in the gain domain (concavity) and risk seeking in the loss domain (convexity). Risk aversion for gains means that decision makers tend to prefer a sure gain of £100 over a gamble offering 50% chance of winning £200 or nothing. Within PT, risk aversion is defined as the preference for a sure outcome over a gamble with higher or equal expected value. Conversely, risk seeking is defined

as the rejection of a sure thing in favour of a gamble of lower or equal expected value (Kahneman and Tversky, 1979; 1984). On the contrary, risk seeking for losses means that people tend to prefer a gamble offering 50% chance of losing £200 or nothing over losing £100 for sure. Moreover, the curvature of the value function is consistent with diminishing sensitivity, the notion that people are more sensitive to changes near the reference point than to changes further away from the reference point. For instance, the difference between a gain/loss of £100 and a gain/loss of £200 has substantially more impact than the difference between a gain/loss of £1100 and a gain/loss of £1200.

Thirdly, the value function is steeper for losses than for gains, which gives rise to loss aversion; the tendency to overestimate losses compared to gains of the same amount as 'losses loom larger than gains' (Kahneman and Tversky, 1979). In the context of decision under risk, loss aversion gives rise to risk aversion for mixed (gain-loss) gambles, so that people typically reject a gamble that offers 50% chance to gain £10 or lose £10.

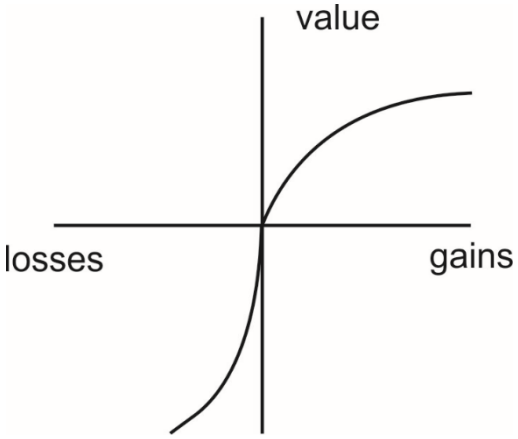


Figure 1.1. The PT value function. Adapted from Kahneman and Tversky (1979).

1.2.2 Probability weighting function

PT assumes probability weighting, the notion that the values of outcomes are not weighted by their objective probabilities but, rather, by decision weights, which represent the impact of the relevant probability of an event on the evaluation and corresponding desirability of a prospect. The decision weight is not necessarily a measure of subjective belief as a person may report that they believe that the objective probability of a fair coin landing heads is ½ but nevertheless give this event a weight of less than ½ in the evaluation of a prospect. The decision weights are computed with a probability weighting function, which is depicted in Figure 1.2.

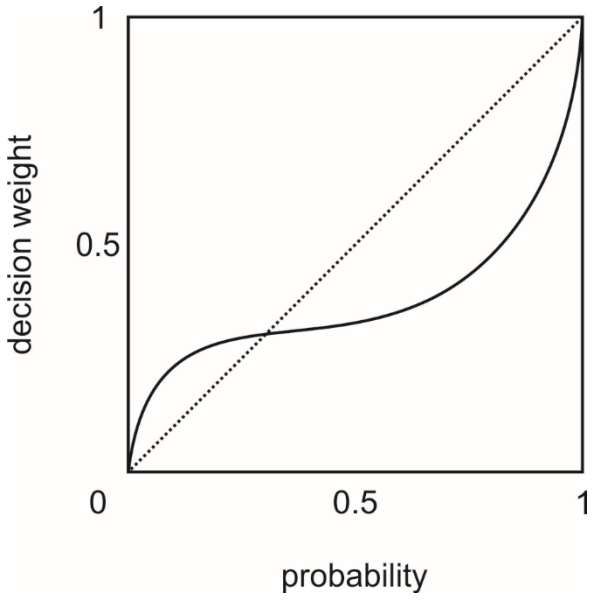


Figure 1.2. The PT probability weighting function. Adapted from Kahneman and Tversky (1979).

The probability weighting function is an inverse S-shaped function that is concave near zero and convex near one. Similar to the value function capturing diminishing sensitivity to changes in the amount of money gained or lost, the weighting function captures diminishing sensitivity to changes in probability, ranging from impossibility to certainty. This shape leads to the fourfold pattern of risk attitudes, so that low probabilities are overweighted, leading to risk seeking for gains

and risk aversion for losses, and moderate to high probabilities are underweighted, leading to risk aversion for gains and risk seeking for losses (Abdellaoui, 2000; Gonzalez and Wu, 1999; Tversky and Fox, 1995; Tversky and Kahneman, 1992). Table 1.1 shows an example of the fourfold pattern of risk attitudes, adapted from Tversky and Kahneman (1992). The certainty equivalent (i.e., the sure payment that the decision maker deems as equally attractive to the risky prospect) of a prospect (x, p) that offers x with probability p is given by $c(x, p)$. Choices consistent with this fourfold pattern have been observed in several studies (Fishburn and Kochenberger, 1979; Hershey and Schoemaker, 1980; Kahneman and Tversky, 1979; Payne et al., 1981). Risk seeking for low probability gains may contribute to the attraction of gambling, whereas risk aversion for low probability losses may contribute to the attraction of insurance. Risk aversion for high probability gains may contribute to the preference for certainty, as in the Allais (1953) paradox, whereas risk seeking for high probability losses is consistent with the tendency to undertake risk to avoid facing a sure loss.

Table 1.1. A fourfold pattern of risk attitudes. Adapted from Tversky and Kahneman (1992).

	Gains	Losses
Low probability	c(£100, 5%) = £14	c(-£100, 5%) = -£8
	Risk seeking	Risk aversion
High probability	c(£100, 95%) = £78	c(-£100, 95%) = -£84
	Risk aversion	Risk seeking

It has been suggested that the fourfold pattern of risk attitudes for (gain-only or loss-only) gambles that offer a gain or a loss with low or high probability is driven primarily by the curvature of the weighting function, because the value function is not particularly curved (Tversky and Kahneman, 1992). Risk aversion for mixed (gain-loss) gambles that offer an equal probability of a gain or loss is driven almost entirely by loss aversion because the curvature of the value function is typically similar for losses versus gains and decision weights are similar for gain versus loss components (Novemsky and Kahneman, 2005). Table 1.2 summarises the main components of PT.

Table 1.2. Summary of the major components of PT. Adapted from Trepel et al. (2005).

Component	Phenomenon	Description	Manifestation
Value function	Sensitivity to gains and losses	Concave for gains / convex for losses	Risk aversion in the gain domain / risk seeking in the loss domain
	Loss aversion	Steeper for losses than for gains	Risk aversion for mixed gambles
Weighting function	Diminishing sensitivity	Convex near 0 Concave near 1	Fourfold pattern of risk attitudes

1.3 Loss aversion

Losses tend to be overvalued compared to gains of the same amount, a phenomenon known as loss aversion (Kahneman and Tversky, 1979). This tendency suggests that the negative affective state that a decision maker experiences by losing a specific amount of money is greater than the pleasure derived by gaining the same amount of money (Kahneman and Tversky, 1979).

In the context of decision making under risk, loss aversion gives rise to risk aversion for mixed (gain-loss) gambles. Within PT, risk aversion refers to a preference for a sure option over a risky prospect as indicated by the curvature of the value function (Kahneman and Tversky, 1979). Decision makers tend to reject fair bets that offer equal chances of winning or losing the same amount of money. For instance, individuals typically reject a 50% chance to gain £100 or lose £100. It is important to note that loss aversion, which relates to the steepness of the value function (for lower values), should be distinguished from risk aversion, which relates to the curvature of the value function, specifically the concavity of value function in the gain domain (Kahneman and Tversky, 1979). As such, risk aversion can occur even without the prospect of a loss. For example, decision makers tend to prefer a sure gain of £5 over a gain-only prospect that offers 50% chance of a £10 gain or £0 otherwise (e.g., Sokol-Hessner et al., 2009). In contrast, loss aversion by definition requires the evaluation of potential negative consequences.

Several studies have demonstrated that loss aversion can be extended from decisions about risky gambles to objects (Kahneman et al., 1990) and ‘mock’

investments (Gneezy and Potters, 1997; Thaler et al., 1997). Additionally, analyses of field data have observed loss aversion for the pricing and purchasing of consumables (Hardie et al., 1993; Putler, 1992), for house investments (Genesove and Mayer, 2001), and even for the choice of work hours by cabdrivers (Camerer et al., 1997). Moreover, it has been proposed that loss aversion might have an evolutionary basis as experiments with primates have demonstrated that they also exhibit loss aversion (Chen et al., 2006). Furthermore, loss aversion is even observed in the trading behaviour of children (Harbaugh et al., 2001), which suggests that it may reflect a fundamental feature of how potential decision outcomes are assessed by the brain. Thus, loss aversion appears to exist across different domains and species. Loss aversion has been used to explain many effects obtained in decision making research, such as the sunk-cost effect (Arkes and Blumer, 1985), the status-quo bias (Knetsch, 1989; Schweitzer, 1994), the endowment effect (Kahneman et al., 1990; Van Dijk & Van Knippenberg, 1998), and the framing effect in negotiations and coalition formation (De Dreu et al., 1994; Van Beest et al., 2005).

Loss aversion is also evident in riskless choice contexts when consumers compare one product attribute against another. For instance, Tversky and Kahneman (1991) asked participants to choose between two hypothetical jobs. The first job was characterised as 'limited contact with others' and a 20-minute daily commute, whereas the second job was characterised as 'moderately sociable' with a 60-minute daily commute. Participants were more likely to choose the first job if they had been told that their present job was socially isolated with a 10-minute commute than if they had been told it was very social but had an 80-minute commute, consistent with the notion that individuals are loss averse for attributes that present relative advantages and disadvantages in comparison to a reference point.

Different theories have been proposed regarding the psychological mechanisms that lead to loss aversion. Some theories describe loss aversion as a 'hedonic property', suggesting that it represents a hedonic preference relative to losses because losses hurt more than gains feel good, such that avoiding a negative affective state is preferred over gaining a positive affective state (Novemsky and Kahneman, 2005). Other theories suggest that loss aversion represents a 'judgmental error' due to an exaggerated fear of losses relative to their actual impact (Camerer, 2005; Kermer et al., 2006), or due to an underestimation of emotional adaptation to negative events

(Wilson and Gilbert, 2005). From this perspective, when an individual is asked to predict how they will feel after experiencing negative outcomes, they tend to anticipate that losses will have a greater impact than they actually do because individuals underestimate their own tendency to rationalise and discount actual losses (Kermer et al., 2006), whereas, in reality, the experience of loss is not as bad as originally anticipated. One fundamental question for the study of decision making is whether loss aversion reflects the engagement of distinct emotional processes when potential losses are considered. It has been suggested that enhanced sensitivity to losses is driven by negative emotions, such as fear or anxiety (Camerer, 2005). In line with this notion, it can be hypothesised that exposure to increasing potential losses should be associated with increased activity in brain structures that are thought to mediate negative emotions in decision making such as the amygdala or anterior insula (Kahn et al., 2002; Kuhnen and Knutson, 2005). Furthermore, loss aversion could reflect an asymmetric response to losses versus gains within a single system that encodes the subjective value of the potential prospect, such as within ventromedial prefrontal cortex (VMPFC), orbitofrontal cortex (OFC) or ventral striatum (VS) (Breiter et al., 2001; Knutson et al., 2003; McClure et al., 2004).

1.3.1 Neurophysiological research on loss aversion

1.3.1.1 Psychophysiological studies

The first study that investigated the neural correlates of loss aversion required participants to make decisions regarding whether they would accept or reject a series of gambles that offered 50% chance of gaining or losing different amounts of money (Tom et al., 2007). Importantly, this study focused on neural responses during the evaluation of potential outcomes, therefore, the gambles were not resolved and participants did not receive any outcomes until the end of the experiment. The study showed that a set of brain areas displayed increasing activity as potential gains increased, including VS, VMPFC, ventrolateral prefrontal cortex (VLPFC), anterior cingulate cortex (ACC), and OFC. There were no brain regions showing decreasing activation as gains increased and no brain regions showing increasing activation as the size of the potential loss increased. Instead, a group of brain regions showed

decreasing activity as the size of potential losses increased. This loss-responsive set of regions included the striatum, VMPFC, ventral ACC and medial OFC. Importantly, the VS and VMPFC exhibited a pattern of neural loss aversion, meaning that they showed joint sensitivity to both gains and losses whereby the slope of the decrease in activity for increasing losses was greater than the slope of the increase in activity for increasing gains. Notably, individual differences in behavioural loss aversion were associated with neural loss aversion in the VS and VMPFC. These results appear to be consistent with the suggestion of PT for a value function that is steeper for losses compared to gains.

Along those lines, Sokol-Hessner et al. (2013) asked participants to accept or reject a series of gambles offering 50% chance of gaining or losing different amounts of money. Participants completed these sets of choices under two cognitive strategies: 'attend' and 'regulate' strategy. In the attend strategy, participants were instructed to consider each choice in isolation, as if it were the only choice in the experiment. In the regulate strategy, participants were asked to consider each choice in a greater context, considering each choice as if it were one of many. The behavioural results showed that the regulate strategy decreased loss aversion compared to the attend strategy. The authors explain this by arguing that, in the regulate strategy, participants evaluated choices and outcomes as part of a broader portfolio, thus, reducing the expected cost of each individual loss. In terms of the fMRI results, at the time of outcome presentation, stronger activity in the amygdala for losses compared to gains was associated with behavioural loss aversion. Furthermore, the reduction of loss aversion by the regulate strategy also correlated with individual differences in the reduction of amygdala activation following losses but not gains.

The above results regarding the effects of the regulate strategy in decreasing loss aversion were supported by another study, in which behavioural loss aversion was associated with stronger skin conductance responses (SCR) to loss outcomes relative to gain outcomes (Sokol-Hessner et al., 2009). Likewise, another study demonstrated increased behavioural loss aversion and SCR to losses during the outcome period while perceiving an unpleasant odour (Stancak et al., 2015).

Amygdala activation has been found to increase as the gain/loss ratio deviates from the individual certainty equivalents (i.e., the point at which participants accepted

and rejected gambles with equal probability). This response pattern has been shown to be more strongly expressed in loss averse individuals, so that amygdala activation was associated with individual differences in loss aversion at the time of choice (Gelskov et al., 2015). Further support for the role of the amygdala in loss aversion comes from a study with individuals with bilateral amygdala lesions (De Martino et al., 2010). The participants completed a set of gambling tasks and showed decreased loss aversion compared to matched controls.

Canessa et al. (2013) observed both bidirectional and gain/loss-specific responses while evaluating gambles, with brain regions such as the amygdala and posterior insula specifically tracking the magnitude of potential losses. Moreover, individual differences in loss aversion were reflected both in limbic fMRI responses and in grey matter volume in a structural amygdala–thalamus–striatum network. Similarly, Canessa et al. (2017) demonstrated that neural responses in the VS and the right posterior insula/supramarginal gyrus during resting state activity were associated with individual differences in behavioural loss aversion evaluated using the gambling task from the study by Tom et al. (2007). Notably, the brain regions which were found to be associated with loss aversion in these two studies were very similar, and cross-study analyses confirmed that this correlation holds when voxels identified were used as regions of interest in task-related activity and vice versa. Taken together, these results suggest that the individual degree of (neural) loss aversion represents a stable individual difference which reflects in specific brain activity at rest and might also modulate cortical excitability at the time of choice.

Furthermore, an association was found between grey matter volume in bilateral posterior insula as well as left medial frontal gyrus with individual loss aversion, so that higher loss aversion was associated with lower grey matter volume in these brain regions (Markett et al., 2016). Another study utilised positron emission tomography (PET) scans and demonstrated a negative correlation between loss aversion and norepinephrine transporters (NET) binding in the thalamus (Takahashi et al., 2012), so that individuals with low thalamic NET showed pronounced loss aversion.

1.3.1.2 EEG studies

EEG studies investigating loss aversion are extremely scarce. Specifically, at the time we started the experiments presented in the current thesis no EEG studies existed on loss aversion. Since then, and to the best of our knowledge, only two EEG studies have been published, one investigating loss aversion during the decision making phase (Heeren et al., 2016) and the other in association with resting state brain activity (Duke et al., 2018).

In the Heeren et al. (2016) study, the authors investigated loss aversion during the decision making phase by comparing ERP responses to easy versus difficult decisions. The gain/loss ratio of gambles was used as a measurement of conflict and difficulty of the decision. Large quotients (i.e., large gains and small losses) mean low decision conflict and attractive gambles. Low quotients (i.e., similar amounts of gains and losses) also mean low conflict because the gamble is clearly unattractive and participants can easily decide to reject it. Decisions with an intermediate difference between offered gains and losses are considered difficult. Results showed that both easy and difficult decisions induced a P300 potential during the evaluation of the available options. However, high conflict decisions were associated with smaller P300 amplitudes compared to low conflict decisions. Importantly, P300 amplitudes were modulated by individual differences in loss aversion such that P300 amplitudes were further reduced for high loss averse participants even in low conflict trials and irrespective of the attractiveness of the gamble. Loss aversion was measured using the task used in the study by Tom et al. (2007). Specifically, participants were asked to accept or reject a series of mixed gambles offering a 50% chance of gaining one amount of money or losing another amount. Loss aversion was calculated for each participant by entering gains and losses into a binary logistic regression analysis as independent variables and predicting the individual decision (accept or reject). Importantly, there were no differences in P300 amplitudes between high and low loss averse participants during high conflict decisions. Hence, the reduced P300 was observed in high loss averse participants even in easy decisions associated with low conflict. Thus, this study demonstrated differences in ERPs between high and low loss averse participants and provided an approximation of the timing at which loss aversion

influences decision making while participants were contemplating potential gains and losses.

In the study by Duke et al. (2018), participants played a gambling task and later their resting state EEG activity was recorded. The authors found that individual differences in loss aversion were associated with increased cortical activity in the right compared to the left hemisphere at central and posterior electrode sites. These findings support the idea that lateralisation of the right hemisphere may underlie individual variation in behavioural loss aversion.

The studies described above have two important shortcomings. Firstly, neither study controlled for the potentially confounding risk aversion effects. As already mentioned, loss and risk aversion can co-occur but they represent distinct properties of PT and affect decision making in different ways. Secondly, both studies utilised an EEG system with only nine electrodes. Although this would not represent an issue for experiments investigating well studied ERP components, in exploratory studies such as these, the use of only nine electrodes is extremely limited and, additionally, it can obstruct any opportunities for source localisation.

Table 1.3 summarises the main findings from the psychophysiological and EEG studies discussed in this section.

Table 1.3. Main findings from psychophysiological and EEG studies of loss aversion.

Study	Method	Participants	Task	Outcome	Results
Tom et al. (2007)	fMRI	16	256 mixed gambles	No	VS, VMPFC
De Martino et al. (2010)	fMRI	8	256 mixed gambles	No	amygdala
Sokol-Hessner et al. (2013)	fMRI	39	240 mixed gambles, 60 gain-only gambles	Yes	amygdala
Canessa et al. (2013)	fMRI	56	104 mixed gambles	No	amygdala, thalamus, striatum
Canessa et al. (2017)	fMRI	57	104 mixed gambles	No	VS, insula
Gelskov et al. (2015)	fMRI	16	128 mixed gambles	No	striatum, amygdala
Markett et al. (2016)	fMRI	41	256 mixed gambles	No	insula
Heeren et al. (2016)	EEG	36	256 mixed gambles	No	P300 attenuation for high loss averse participants
Duke et al. (2018)	EEG	40	256 mixed gambles	No	alpha band asymmetry at central and posterior sites
Sokol-Hessner et al. (2009)	SCR	29	240 mixed gambles, 60 gain-only gambles	Yes	SCR differences in arousal to losses versus gains
Stancak et al. (2015)	SCR	30	240 mixed gambles, 60 gain-only gambles	Yes	unpleasant odour increased loss aversion
Takahashi et al. (2012)	PET	19	40 mixed gambles	No	higher loss aversion in individuals with lower NET in the thalamus

1.3.2 Phenomena related to loss aversion

It has been suggested that loss aversion leads to a range of behavioural phenomena (e.g., Kahneman et al., 1991). One such phenomenon is the endowment effect, which refers to the notion that people often demand much more money in order to part with a possession compared to the amount of money that they would be willing to pay in order to acquire it (Thaler, 1980). The endowment effect has been demonstrated in several experiments using a variety of objects. In a classic experiment by Kahneman et al. (1990), half of the participants were given coffee mugs and the other half were given pens of equal monetary value. Participants who were given mugs were reluctant to trade their mug for pens, and similarly, participants who were given pens were reluctant to trade them for coffee mugs. The endowment effect has generally been interpreted as a manifestation of loss aversion on the assumption that once an object has been acquired, the pain associated with parting with that object is larger than the pleasure associated with exchanging it for another equally priced object (Kahneman et al., 1990; Thaler, 1980; Van Dijk and Van Knippenberg, 1996).

Variations of the above experiments included investigating the discrepancies between willingness to pay (WTP) and willingness to accept (WTA) prices. In these experiments, half of the participants were endowed with an item (e.g., coffee mugs, chocolate bars) while the remaining half were not endowed with anything (Kahneman et al., 1990). Participants that were endowed with the item ('sellers') were informed that they could sell the object in their possession to one of the participants who were not endowed with an item ('buyers'). It was found that sellers demanded much higher prices to part with the object compared to the amount of money that buyers were offering to acquire the same object. The authors concluded that the endowment effect does not reflect the appeal of the good one owns but, rather, reflects the pain of parting with the good, so that the disutility of giving up an object is greater that the utility associated with acquiring it. Of course, it must be noted that loss aversion does not affect transactions with goods that were initially intended for sale (Novemsky and Kahneman, 2005).

A study investigating the neural basis of the endowment effect found that WTP prices were associated with VMPFC activation, whereas WTA prices were associated with OFC activation (De Martino et al., 2009). Overall, the ventral striatum showed a

pattern indicative of the endowment effect being more activated during selling compared to buying trials. Importantly, individual differences in the endowment effect (i.e., WTA/WTP differences) were associated with bilateral ventral striatal activity. Additionally, Plassmann et al. (2007) utilised an auction paradigm which compared free-bid trials, in which participants decided how much to bid on a food item, with forced-bid trials, in which participants were told how much to bid. Results showed that activity in VMPFC and DLPFC was associated with WTP in the free-bid trials but not the forced-bid trials, suggesting that these regions are particularly involved in coding for decision utility. Subsequent work using WTP paradigms has confirmed that the VMPFC activation is associated with decision utility across a broad range of goods (Chib et al., 2009), suggesting that the VMPFC serves as a common pathway for value representation.

Similarly, De Martino et al. (2006) manipulated framing during a decision making task in which participants chose between a sure outcome and a gamble after receiving an initial endowment on each trial. Framing was manipulated by offering participants the choice between a sure loss and a gamble (loss frame; e.g., lose £30 versus gamble) or the choice between a sure gain and a gamble (gain frame; e.g., keep £20 versus gamble). Participants showed risk seeking in the loss frame and risk aversion in the gain frame. Amygdala activation was associated with the dominant choices, with increased activity for sure choices in the gain frame and risky choices in the loss frame. The dorsal ACC displayed the opposite pattern across conditions. Individual differences in behavioural framing-related bias were correlated with framing-related activation in right OFC and VMPFC, so that participants who showed less framing bias showed more activity for sure choices in the gain frame and risky choices in the loss frame compared to the other two conditions. Thus, whereas amygdala showed the framing-related pattern across all participants, in the OFC this pattern was stronger for participants who showed less of a behavioural framing effect.

1.4 Evaluation of decision outcomes in the brain

It is evident from the previous sections that loss aversion manifests in response to anticipated and experienced negative outcomes (e.g., Sokol-Hessner et al., 2013; Tom et al., 2007). Accordingly, it has been hypothesised that the striatum represents loss aversion at the time of a binary choice between a gamble or a sure outcome by encoding the values assigned to prospective outcomes (Tom et al., 2007) and that these values are then processed by the amygdala so that the amygdala represents loss aversion at the time of outcome receipt (Sokol-Hessner et al., 2013). The implication of the striatum and the amygdala in reward evaluation is supported by several fMRI studies which have aimed to identify the brain regions that encode value, both during the decision making phase and during the receipt of the decision outcome phase. Meta-analyses of those studies (Bartra et al., 2013; Kringelbach, 2005; Lebreton et al., 2009; Padoa-Schioppa and Conen, 2017) suggest that the VS, the amygdala, the VMPFC, the posterior cingulate cortex (PCC), and the OFC are the main brain regions that collectively form the brain's valuation system. Activation in these regions tends to increase when considering the subjective value of the available options during choice, as well as with the value of the reward received, thus, implicating a common set of brain regions in the evaluation of both prospects and outcomes (Bartra et al., 2013). Importantly, these brain regions have been found to respond to outcomes in multiple domains, including both primary rewards (e.g., food) and secondary rewards (e.g., monetary or social rewards), suggesting that the valuation system is domain-general (Delgado, 2007; Grabenhorst and Rolls, 2011; Kable and Glimcher, 2009; Knutson and Cooper, 2005; Levy and Glimcher, 2012; Montague and Berns, 2002; O'Doherty et al., 2004; Peters and Büchel, 2010).

1.5 ERP correlates of decision outcomes

This section describes the spatiotemporal aspects of the neural evaluation of decision outcomes by focusing on EEG research. Although there is undoubtedly a range of ERP components that might be associated with outcome evaluation, the two components prevailing in the literature are feedback-related negativity (FRN) and P300.

1.5.1 FRN

FRN is one of the most extensively studied ERPs in the reward processing literature (Walsh and Anderson, 2012). It is commonly elicited by experimental paradigms that employ forced-choices between two gambles which are subsequently followed by presentation of gain or loss feedback (Gehring and Willoughby, 2002; Hajcak et al., 2006; Holroyd et al., 2006; Nieuwenhuis et al., 2004b; Yeung and Sanfey, 2004). FRN is typically evaluated as the difference waveform between averaged potentials time-locked to the presentation of gain and loss outcomes (Gehring and Willoughby, 2002). The resulting potential difference has a fronto-central scalp distribution and its maximum amplitude occurs between 200-350 ms after feedback presentation (Walsh and Anderson, 2012). The brain region that has most often been suggested to contribute to the generation of the FRN is the ACC (Bellebaum and Daum, 2008; Cohen and Ranganath, 2007; Gehring and Willoughby, 2002; Hewig et al., 2007; Miltner et al., 1997; Potts et al., 2006; Ruchsow et al., 2002; Tucker et al., 2003; Zhou et al., 2010). Other sources that have also been suggested as the potential neural generators of the FRN include the PCC (Badgaiyan and Posner, 1998; Cohen and Ranganath, 2007; Donamayor et al., 2011; Luu et al., 2003; Müller et al., 2005; Nieuwenhuis et al., 2005c) and the striatum (Carlson et al., 2011; Foti et al., 2011; Martin et al., 2009).

The two experiments that first identified the FRN component were conducted by Miltner et al. (1997) and Gehring and Willoughby (2002). Miltner et al. (1997) utilised a time estimation task in which participants had to estimate the duration of 1 s. At the beginning of the task a tolerance window of ± 100 ms was used during which a response was considered a correct response. This window was adjusted for each trial based on participants' responses so that when they guessed correctly, the window decreased by 10 ms, whereas when they were incorrect, the window was increased by 10 ms. Following their responses, participants received feedback as to whether their guess was correct in the form of visual, auditory or tactile stimulus. By comparing the average correct and incorrect waveforms, the authors observed an ERP component evoked by performance feedback peaking approximately 250 ms after stimulus onset. This component was elicited irrespective of the modality in which feedback was provided.

In the experiments conducted by Gehring and Willoughby (2002), a monetary gambling task was employed whereby participants made choices between two cards associated with 50% chance of winning or losing money. Following their choice, participants received feedback about whether the gamble resulted in gain or loss. By comparing grand average ERPs to gain and loss trials, the authors observed a negative-polarity ERP component, peaking approximately 265 ms after feedback onset, which was stronger for loss compared to gain trials. The Gehring and Willoughby (2002) gambling task is the most commonly used task for FRN elicitation and studies using comparable experimental paradigms have consistently found FRN following monetary losses (Hajcak et al., 2005; Holroyd et al., 2004; Nieuwenhuis et al., 2004; Yeung et al., 2005; Yeung and Sanfey, 2004).

A range of theoretical accounts have been proposed to explain the generation of FRN (Botvinick et al., 2001; Yeung et al., 2004). The most influential theory has been the FRN reinforcement learning theory, which postulates that the FRN reflects a reinforcement learning reward prediction error (Holroyd and Coles, 2002). According to the theory, the ACC, the midbrain dopamine system and the basal ganglia form a reinforcement learning system within the medial-frontal cortex (Schultz, 2002). Discrepancies between expected and received outcomes (i.e., reward prediction errors) are computed by the basal ganglia and then conveyed to the ACC through the midbrain dopamine system. In this way, the dopamine system monitors outcomes to determine whether things have gone better or worse than expected. Outcomes that are better than expected (i.e., positive prediction errors) induce phasic increases in the dopamine firing rates of a mesencephalic dopamine system, producing smaller FRN amplitudes. Outcomes that are worse than expected (i.e., negative prediction errors) induce phasic decreases, producing stronger FRN amplitudes. These signals are thought to guide action selection mediated by the ACC, through the reinforcement of the action associated with positive outcomes and the punishment of the action associated with negative outcomes.

1.5.1.1 Outcome valence

The most robust finding in the FRN literature is that the FRN component is primarily modulated by outcome valence. For instance, several studies have

consistently reported the presence of the FRN component when participants receive negative compared to positive performance feedback (Hajcak et al., 2005; Hajcak et al., 2006; Holroyd and Coles, 2002; Holroyd et al., 2004; Luu et al., 2003; Nieuwenhuis et al., 2004b; Ruchsow et al., 2002; Yeung et al., 2005; Yeung and Sanfey, 2004). The FRN also occurs following the presentation of stimuli indicating monetary loss or non-reward compared to reward (Gehring & Willoughby, 2002; Hajcak et al., 2005, 2006; Holroyd et al., 2006; Yeung et al., 2005; Yeung & Sanfey, 2004). Therefore, FRN can be elicited following both performance and monetary feedback (Gehring and Willoughby, 2002; Hajcak et al., 2005; Luu et al., 2003; Miltner et al., 1997; Yeung et al., 2005; Yeung and Sanfey, 2004). Nieuwenhuis et al. (2004b) compared these two feedback types within a single study and demonstrated that FRN could be elicited by either utilitarian (monetary loss) or performance (incorrect response) information, even within the same decision context. Specifically, when feedback included information about both dimensions simultaneously, the aspect of the feedback that elicited the FRN was the one that had been emphasised to participants. These findings suggest that monetary losses and negative performance feedback can be considered functionally equivalent because both reflect outcomes along a good-bad dimension.

Furthermore, it has been suggested that the FRN is context-dependent (Holroyd et al., 2004). For example, feedback indicating that participants received no reward elicited FRN when the alternative outcomes were rewards. However, the same feedback did not generate FRN when the alternative outcomes were monetary losses. Thus, FRN was elicited by unfavourable outcomes, however, what constituted an unfavourable outcome was determined by the alternative feedback within the given task context. Taken together, the above findings suggest that FRN categorises outcomes in a binary manner by distinguishing between good and bad or better and worse than expected outcomes (Hajcak et al., 2006).

1.5.1.2 Outcome probability

Another factor that has been shown to modulate FRN amplitude is outcome probability. Some researchers have suggested that FRN amplitude is stronger for improbable (unexpected) compared to probable (expected) negative outcomes. For

instance, in a study by Hajcak et al. (2007), participants were presented with four doors and were instructed to guess which door hid a prize, with the goal of winning as many prizes as possible. Prior to each trial, a cue was presented indicating how many doors hid a prize (1, 2 or 3). Thus, the probability of positive feedback could be inferred from this cue (25%, 50%, or 75%, respectively). Following their choice, participants received feedback about whether they had guessed correctly. FRN was the most negative following improbable events (i.e., associated with small probabilities), in that it was the most negative in trials associated with 75% probability to receive rewards. Other studies utilising variations of the Hajcak et al. (2007) task have also provided support for a modulation of FRN by outcome probability (Bellebaum and Daum, 2008; Bellebaum et al., 2010b; Cohen et al., 2007; Hewig et al., 2007; Holroyd and Krigolson, 2007; Holroyd et al., 2011; Holroyd et al., 2003; Kreussel et al., 2012; Liao et al., 2011; Martin and Potts, 2011; Martin et al., 2009; Potts et al., 2006; Walsh and Anderson, 2011). Nevertheless, other experiments have not found support for such a reward probability modulation (Hajcak et al., 2005).

1.5.1.3 Outcome magnitude

When considering the modulation of FRN by reward magnitude, it has been suggested that the evaluative system could determine the favourableness of events according to the value of the feedback, so that large losses should elicit an enhanced FRN relative to small losses, and small gains should elicit a larger FRN compared to large gains (Holroyd et al., 2004). Alternatively, FRN might reflect the binary categorisation of good versus bad outcomes, so that an event is simply categorised as either good or bad (Yeung and Sanfey, 2004). Although it appears to be intuitive that an outcome evaluation system would be influenced by outcome magnitude, many studies fail to find such a modulation regarding FRN (Goyer et al., 2008; Hajcak et al., 2006; Marco-Pallarés et al., 2008; Masaki et al., 2006). Furthermore, in the studies that manipulated reward magnitude and found support for such a modulation (Bellebaum et al., 2010b; Holroyd et al., 2004; Kreussel et al., 2012), outcome values were known in advance (Nieuwenhuis et al., 2004a). Therefore, it is possible that the monitoring system might scale its response to negative feedback based on the potential outcomes on each trial, so that losing 5 when 5 could have been won may be similar

to losing 10 when 10 could have been won. Several fMRI studies have demonstrated that, in such circumstances, the brain displays adaptive scaling. Neural firing rates and BOLD responses adapt to the range of outcomes so that maximum deviations from baseline remain constant regardless of absolute reward values (Bunzeck et al., 2010; Nieuwenhuis et al., 2005a; Tobler et al., 2005). Failure to find an effect of reward magnitude on FRN strength might indicate that the FRN also scales with the range of reward values (Nieuwenhuis et al., 2004a).

To further investigate the possibility of FRN modulation by reward magnitude, Hajcak et al. (2006) employed a paradigm in which participants did not know in advance whether the potential reward would be small or large. Specifically, participants performed a gambling task in which four outcomes that varied in magnitude and valence were equally likely to be presented as feedback. For each trial, participants could gain 25, gain 5, lose 5, or lose 25. FRN was consistently observed following monetary loss, but FRN magnitude was insensitive to the magnitude of the loss. In a second experiment, the authors included a condition in which participants could break even (i.e., receive nothing). Results showed that feedback indicating that participants had broken even did not elicit FRN with a magnitude intermediate to gains and losses. Rather, the FRN observed following zero feedback was similar in magnitude to the FRN following losses. In addition, large and small losses both elicited equally large FRN. These results support the idea that the FRN reflects a coarse differentiation of favourable versus unfavourable outcomes (Yeung and Sanfey, 2004).

1.5.1.4 Counterfactual outcomes

The research described up to here has focused on the evaluation of obtained decision outcomes. However, in order to determine whether the decision made led to the best possible outcome, decision makers often need to compare the obtained outcome with other possible outcomes that could have been obtained, if they had chosen differently. This comparison process is generally referred to as ‘counterfactual thinking’ (Roese and Olson, 1993). When counterfactual comparisons indicate that the obtained outcome could have been better if another decision had been made, this can lead to negative feelings, including regret or disappointment. When counterfactual

comparisons show that the obtained outcome could have been worse, this can lead to positive feelings, including elation or satisfaction (Roese and Epstude, 2017). In gambling tasks, a counterfactual comparison can generally be evoked by feedback informing participants about both the received outcome and the alternative possible outcome (Osinsky et al., 2014). Along those lines, it has been hypothesised that FRN might categorise counterfactual outcomes in a way that corresponds to the encoding of actually obtained outcomes, so that missed desirable outcomes are counterfactually evaluated as losses and missed undesirable outcomes are counterfactually evaluated as gains (Roese and Epstude, 2017). However, FRN literature on this topic does not provide comprehensive results. Although some studies suggest that missed gains are indeed experienced as losses, whereas escaped losses are experienced as gains (Gu et al., 2011; Yu and Zhou, 2009), others fail to find such a differentiation between counterfactual outcomes (Marciano et al., 2018; Yeung and Sanfey, 2004; Yu and Zhou, 2009). Finally, others propose that both chosen and unchosen outcomes are processed similarly, such that FRN encodes only positive or negative valence (Osinsky et al., 2014). Therefore, it is clear that more research is needed on this topic in order to fully understand the spatiotemporal characteristics of counterfactual thinking, and this could be achieved by using the EEG technique. The role of FRN in the processing of missed outcomes was further investigated in the second study (detailed in Chapter 4).

1.5.1.5 Free versus obstructed choices

Another open question concerning the role of FRN in decision making is how this component encodes outcomes that were not freely chosen by individuals. The research described in previous paragraphs investigated decision making under unobstructed choice conditions, thus, allowing participants to freely select among available prospects (Gehring and Willoughby, 2002; Goyer et al., 2008; Hajcak et al., 2006, 2007; Holroyd et al., 2004; Nieuwenhuis et al., 2004b). Even though it is undeniably important to understand the neural mechanisms of free choice, perhaps it is even more crucial for real world decision making to also understand choice under conditions of unexpected circumstances that force us to change the path of our decision

making. The role of FRN in the processing of unpredictable and unchosen outcomes formed the topic of the third study (detailed in Chapter 5).

1.5.1.6 Social context

Social context during decision making is an important factor that could influence FRN. Social comparison, which is intuitively at the core of feelings associated with upward counterfactuals, might play a role in outcome evaluation even in situations where the good fortune of another individual does not affect the fortune of the participant (Dvash et al., 2010). The effects of making decisions for others and processing of vicarious rewards on FRN have been shown to be modulated by empathy (Liu et al., 2018) or by social distance (Leng and Zhou, 2014). The role of FRN in a social context whereby participants made decisions either for themselves or for others formed the topic of the fourth study (detailed in Chapter 6).

1.5.1.7 Methodological issue

An important methodological issue that needs to be considered when investigating FRN is that this component is typically evaluated as the difference potential waveform between the canonical ERP waveforms following gains and losses (Luck, 2014). Therefore, whether the resulting difference waveform has a positive or negative valence will depend on the subtraction performed: it will have a negative polarity if losses are subtracted from gains and a positive polarity if the inverse subtraction is performed, meaning that FRN represents a relative rather than an absolute negativity. This often produces confusion in the literature, mainly because of the component nomenclature (Krigolson, 2017). In the initial FRN experiments (Gehring and Willoughby, 2002; Miltner et al., 1997), the component was named as such because of the negative shift that could be observed only on the loss but not on the gain canonical feedback ERP waveforms. Furthermore, initial investigations considered FRN to represent a variation of the error-related negativity (ERN); a component that indexes internal error representations when external feedback is not necessary in order to evaluate whether an action has been successful or unsuccessful

(Falkenstein et al., 1991; Gehring et al., 1993). The similarities in the elicitation and topography of FRN with ERN have led several researchers to consider that the two components are part of the same error detection mechanism (Krigolson, 2017). Furthermore, some researchers have suggested that it is positive, rather than negative, feedback that modulates the FRN, and suggested that the component should instead be referred to as reward positivity (Proudfit, 2015). Therefore, one needs to keep in mind that the subtraction performed will not influence the conclusions drawn regarding the experimental findings, rather, it will only influence whether the final component is graphically represented as a negativity or a positivity.

1.5.2 P300

In addition to FRN, another ERP component that has been suggested to play an important role in outcome evaluation and reward processing is the P300; a positive shift in the electrocortical potential occurring approximately 300-500 ms after stimulus onset and acquiring its maximum amplitude at parietal scalp locations (Polich, 2007, 2012). The P300 has been one of the most studied ERPs since it was first reported (Sutton et al., 1965), and is thought to be associated with several cognitive and affective processes, including information processing and attention allocation (Donchin et al., 1978; Duncan-Johnson and Donchin, 1977; Polich, 2007).

Early P300 studies investigated the role of stimulus probability and task relevance by utilising oddball paradigms (Donchin et al., 1978; Pritchard, 1981). The oddball task presents two different stimuli in a random sequence, with one occurring less frequently (target) than the other (standard), and participants are instructed to respond only to the target stimulus. Discriminating the target stimulus from the standard stimulus produces a P300 component that increases in amplitude as the probability of occurrence of the target stimulus decreases (Duncan-Johnson and Donchin, 1982; 1977). Subsequent studies investigated the role of attentional resource allocation, by employing dual-task performance paradigms in which a primary task is performed while the participant is also engaged in a secondary task of mentally counting target oddball stimuli. P300 amplitude from the oddball task decreases as the difficulty of the primary task increases (Kramer et al., 1985; Wickens et al., 1983). For tasks that require large compared to small amounts of attentional resources, the

P300 amplitude is relatively small and the peak latency is later because processing resources are being used for task performance (Polich, 2003).

The generation of the P300 has been explained within the context-updating theory (Donchin, 1981; Polich, 2003). This theory proposes that the P300 component is associated with the revision of the mental representations induced by stimuli. After initial sensory processing, a comparison process evaluates the representation of the previous event in working memory in order to ascertain whether the current stimulus is either the same as the previous stimulus or not. For instance, in the oddball task, the comparison process is employed to determine whether a standard or a target stimulus was presented. If no differences in the stimulus are detected, the current mental model of the stimulus context is maintained, and only sensory evoked potentials are generated (N100, P200, N200). If a new stimulus is detected, the subject allocates attentional resources to the target, and the neural representation of the stimulus environment is changed or updated, so that a P300 potential is generated in addition to the sensory evoked potentials.

Importantly, P300 has also been observed in tasks involving decision making and outcome evaluation and is thought to reflect the evaluation of the functional significance of feedback stimuli (Hajcak et al., 2005; 2007; Sato et al., 2005; Toyomaki and Murohashi, 2005; Yeung et al., 2005; Yeung and Sanfey, 2004). Specifically, in the context of value-based decision making, P300 has been consistently shown to be sensitive to the magnitude of the reward, being more positive for larger compared to smaller rewards (Bellebaum et al., 2010b; Gu et al., 2011; Sato et al., 2005; Wu and Zhou, 2009; Yeung and Sanfey, 2004). In addition to reward magnitude, studies have demonstrated that the P300 is also sensitive to reward valence, being more positive for gain compared to loss feedback (Bellebaum et al., 2010b; Hajcak et al., 2005; 2007; Holroyd et al., 2004; Leng and Zhou, 2010; Li et al., 2010; Wu and Zhou, 2009; Yeung et al., 2005). Nevertheless, other studies found no support for P300 amplitude modulation by outcome valence (Sato et al., 2005; Yeung and Sanfey, 2004). Finally, similarly to studies that utilised the oddball paradigm (Courchesne et al., 1977; Duncan-Johnson and Donchin, 1977; Johnson and Donchin, 1980), studies employing gambling tasks have also found that P300 is modulated by outcome probability, so that unexpected rewards elicited stronger P300 amplitudes

compared to expected rewards (Cohen et al., 2007; Hajcak et al., 2005; 2007; Holroyd and Krigolson, 2007; Holroyd et al., 2003).

Motivated by research demonstrating that FRN is typically sensitive to reward valence whereas the P300 is sensitive to reward magnitude, it has been proposed that the FRN and the P300 components might encode different aspects of outcome evaluation (Kamarajan et al., 2009; Sato et al., 2005; Toyomaki and Murohashi, 2005; Yeung and Sanfey, 2004; Yu and Zhou, 2006). In particular, it is possible that the FRN serves as an early automatic evaluation process that coarsely differentiates between good and bad outcomes, whereas the P300 is a later cognitive/affective appraisal process for which factors related to the allocation of attentional resources, including reward valence and magnitude, are of importance (Yeung and Sanfey, 2004).

1.6 Interim summary

In light of the research discussed in the previous sections, it is evident that loss aversion plays a profound role in decision making. Brain regions that are important for value computation and reward processing have also been suggested to encode loss aversion. Given the definition of loss aversion as a cognitive bias towards potential losses and the sensitivity of FRN in differentiating between gain and loss outcomes, FRN provides a suitable candidate to investigate the neural underpinnings of loss aversion during the outcome receipt phase of the decision making process.

1.7 Research problems

Although loss aversion has been proven to be a robust behavioural phenomenon, the neural mechanisms underlying its influence on decision making and evaluation of decision outcomes are still poorly understood due to the limited amount of neuroimaging studies, especially those employing EEG. Most importantly, the temporal aspects of loss aversion effects on decision making and outcome evaluation are an important, yet still not investigated, topic. Moreover, little is known about whether loss aversion measured at the time of the decision influences subsequent evaluation of decision outcomes during the learning of the outcome phase. It is not

clear if (and which) ERP components are associated with loss aversion, and specifically the timing of such modulation. Furthermore, the majority of existing neuroimaging research did not control for potential risk aversion effects, which is a possible source of confound in both the behavioural and the neuroimaging data. Such questions have wider relevance for the general literature on risky decision making and reward evaluation, and can only be investigated using a neuroimaging technique with high temporal resolution, such as EEG. The first experimental study of the current thesis, which is described in detail in Chapter 3, served as a starting point towards answering these questions.

Additionally, it is not known whether potential loss aversion effects exert similar modulation on outcome evaluation during simple decisions and during more complex decision situations. The second experiment (detailed in Chapter 4) aimed to compare two different types of undesirable outcomes; experienced losses and missed gains. To this end, participants were prompted to engage in comparisons relating to counterfactual thinking and processing of missed opportunities. Given that loss aversion is a bias towards avoiding negative outcomes, it might correspondingly affect the processing of missed opportunities, if these are perceived as negative prospects. This topic has great importance for decision making research as not only are we frequently required to make decisions by simultaneously considering alternative options, but also we are often confronted with regret associated with wrong decisions. Furthermore, there is also the potential of anticipated regret about making the wrong decision such that regret can occur both before and after making a decision.

Furthermore, decision making is often limited by the amount of freedom (or lack thereof) that the decision maker has. The role of loss aversion is of evident relevance in such a context as decision makers can be inflicted by losses irrespective of whether these losses were the consequence of their own freely-made choices or not. This topic of obstructed, relative to free, decision making was investigated in the third experimental study (detailed in Chapter 5).

Finally, in order to understand how decisions might differ depending on the recipient of the decision outcome, the fourth study (detailed in Chapter 6) investigated loss aversion within a social context. Loss aversion and corresponding outcome evaluation patterns were directly compared in two decision making situations; in one,

participants made a series of gambling decisions for themselves and kept the rewards earned, whereas in the other they gambled for another participant and gave their earnings to that participant.

1.8 Aims

The main aims of the current thesis were: 1) to investigate the neural correlates of loss aversion at the time of receiving a decision outcome, 2) to identify the timing of potential loss aversion effects by taking advantage of the temporal resolution of the EEG technique, 3) to ensure that the observed results pertained only to loss aversion by utilising an incentivised gambling paradigm that allowed a simultaneous separation of loss and risk aversion, and 4) to explore specific conditions under which such influences do and do not occur.

1.9 Hypotheses

- Individuals with large loss aversion will show stronger FRN amplitude compared to individuals with small loss aversion (study 1).
- Individual differences in loss aversion will be correlated with FRN amplitude strength following actual outcomes but not with FRN following counterfactual outcomes (study 2).
- Individual differences in loss aversion will be correlated with FRN amplitude following outcomes resulting from free choices but not with FRN amplitude following outcomes resulting from choices that were arbitrarily imposed on participants (study 3).
- Individual differences in loss aversion will be correlated with FRN amplitude following outcomes obtained for participants themselves but not with FRN amplitude following outcomes obtained for others (study 4).

Chapter 2

General Methods

2.1 Loss aversion estimation

Several methods have been used in behavioural and neuroimaging experiments in order to evaluate loss aversion. The main methods fall broadly into the following categories:

2.1.1 Questionnaires

The first efforts to obtain loss aversion estimates utilised short questionnaires in which participants selected their preferred option between a set of choice problems (Kahneman and Tversky, 1979). The problems presented symmetric bets offering equal probability to win or lose the same amount of money, based on the idea that if these bets are considered unattractive this would be evidence for loss aversion (Kahneman and Tversky, 1979). Subsequent experiments asked participants to rate the acceptability of pairs of mixed prospects (e.g., 50% chance to lose £100 and 50% chance to win an alternative amount) in which the alternative amount varied over trials (Tversky and Kahneman, 1992). Variations of these problems consisted of comparing a fixed prospect (e.g., 50% chance to lose £20 and 50% chance to win £50) to a different set of prospects (e.g., 50% chance to lose £50 and 50% chance to win *x*) in which *x* varied from trial to trial.

2.1.2 Endowment paradigms

Another set of experiments focused on loss aversion in riskless contexts based on the idea that people tend to value objects more after they come to feel that they own them, a phenomenon known as the endowment effect (Thaler, 1980; Tversky and Kahneman, 1991). This has the implication that the minimum amount of money that

a person is willing to accept to part with an object generally exceeds the minimum amount of money that the person is willing to pay to obtain the same object, and these differences between WTA-WTP values are interpreted as evidence for loss aversion (Kahneman et al., 1991; Novemsky and Kahneman, 2005). For instance, Kahneman et al. (1990) presented a coffee mug to one group of participants ('sellers'), told them that the mug was theirs to keep, and then asked them to state the minimum WTA amount to give up the mug. A second group of participants ('buyers') were told that they had the option of receiving an identical mug or an amount of money and asked which they preferred at various prices. The sellers quoted higher prices compared to the buyers, presumably because the former framed the choice as a loss of a mug against a gain of money, whereas the latter framed the choice as a gain of a mug against a gain of money (Kahneman et al., 1990). These findings have been replicated in similar endowment paradigms using a variety of products, including lottery tickets (Knetsch and Sinden, 1984), basketball tickets (Carmon and Ariely, 2000), gift vouchers (Sen and Johnson, 1997), snack choices (Levin et al., 2002), chocolate (Kahneman et al., 1991), and wine (Van Dijk and Van Knippenberg, 1998).

2.1.3 Gambling/choice tasks

This category differs from questionnaires in that the tasks did not rely solely on a small (typically less than ten) number of gambling choices but rather systematically employed a range of carefully selected amounts of money in order to achieve more robust individual decision making parameters that were not influenced by the specific selection of gambling stakes. Tasks within this category can be further divided into non-parametric and parametric methods.

2.1.3.1 Non-parametric

Non-parametric methods do not make any assumptions regarding the form of the value and probability weighting functions. These methods rely on a two-stage process whereby the value function is estimated first and then it is used to estimate the probability weighting function. One of the most commonly used non-parametric methods for loss aversion estimation entails asking participants to choose between a

number of two-outcome gambles associated with different probabilities with the goal to assess certainty equivalents for each choice (Gonzalez and Wu, 1999). Each gamble offers a 50% chance to win a specified amount of money or nothing versus a sure smaller amount. For instance, assuming a gamble prospect of £100 or £0, if a participant preferred a sure prospect of £40 over the gamble, but preferred the gamble over a sure prospect of £20, then the following round of choices would be designed such that it reduces the range to be between £40 to £20. This process is repeated until exact certainty equivalents can be estimated. That is, if a participant preferred a sure £36 over a gamble, but preferred the gamble over £35, then a certainty equivalent for this participant is £35.5. Each possible outcome amount and probability weight are parameters that are estimated using a least squares procedure whereby each step either held weight constant and estimated value or held the value constant and estimated weight.

Another commonly used non-parametric example is the trade-off method (Wakker and Deneffe, 1996). This method requires participants to choose between a pair of two-outcome prospects. The prospects offer a specified probability to win an amount of money or an alternative amount for sure (e.g., win x with probability p or receive y for sure), with one of the outcomes being adjusted following each choice. For instance, a participant might be offered a choice between a fixed 50% probability to win £100 or £20 for sure versus 50% to win £70 or £40 for sure. If the participant prefers the latter gamble, then the variable prospect of the first gamble (e.g., the £100 amount) will increase or decrease (e.g., £110). This amount will vary until both prospects are equally attractive for the participant. Once indifference is established for a first pair of prospects, the procedure continues with a second pair of prospects with the same probability and reference outcomes but with a different variable outcome. By combining the two indifference values, equal value intervals can be estimated such that a standard set of equally spaced outcomes can be produced, creating a parameter-free value function for gains. The disadvantage of non-parametric methods is that they are generally quite cognitively demanding for participants, requiring choices between multiple two-outcome prospects (or even more complicated choices).

2.1.3.2 Parametric

In parametric approaches, specific functional forms for the value and probability weighting functions are fitted directly to the obtained choice data. One such method entails asking participants to choose whether they want to accept or reject a series of mixed-gambles offering 50% chance of winning or losing different amounts of money (Tom et al., 2007). In order to estimate individual differences in sensitivity to gains and losses, a logistic regression is performed on each participant's choice data with the potential gain and loss amounts as independent variables and participant's decision (accept vs reject gamble) as the dependent variable, thus leading to separate measurement of sensitivity to gains and losses (the regression coefficients). A measure of loss aversion can then be computed as the ratio of the loss response to the gain response, such that loss aversion equals $-\beta_{loss} / \beta_{gain}$, where β_{loss} and β_{gain} are the unstandardised regression coefficients for the loss and gain variables, respectively. This method does not take into account the PT value and weight functions. This method assumes a piecewise linear value function, and identical decision weights for a 50% probability to gain or lose money. This method has been used almost exclusively in neuroimaging research for the estimation of loss aversion (Canessa et al., 2017; 2013; De Martino et al., 2010; Duke et al., 2018; Heeren et al., 2016) as it is easy to implement within a neuroimaging experiment. However, this method has the disadvantage that it does not allow for separate estimation of risk aversion. It has been proposed that loss aversion and risk aversion are often confounded (Sokol-Hessner et al., 2009) and this might lead to mistaken assumptions regarding the source of the obtained choices and corresponding brain activation.

A modification of this method has been proposed in order to accommodate an estimation of risk aversion (Sokol-Hessner et al., 2009). This method requires participants to make two different types of choices that each allow the estimation of either loss or risk aversion. Specifically, for the loss aversion estimation, participants are required to choose between mixed-gambles offering 50% chance of winning or losing different amounts of money and a sure zero outcome. For the risk aversion estimation, participants are required to choose between gain-only gambles versus a sure non-zero outcome, which is smaller than the gain from the corresponding gamble in each trial. The rationale for this is that risk aversion can be present even without the

prospect of potential loss, whereas loss aversion by default requires the measurement of loss outcomes. Importantly, this method allows for a behavioural separation of loss and risk aversion, and researchers can separately investigate the brain processes underlying specifically each of these variables by including only the neuroimaging data from each type of trials. This is the method that was chosen for the experiments presented in the current thesis, and a detailed description of the task and the estimation procedure used are given in Chapter 3.

2.2 Electroencephalography (EEG)

2.2.1 Physiological basis of the EEG signal

Neurons in the brain communicate with each other through discrete voltage spikes, known as action potentials. These action potentials travel from the cell body along the axons towards excitatory or inhibitory terminals called dendrites (Speckmann and Elger, 2005). When action potentials reach the dendrites, neurotransmitters are released which bind with the receptors of the postsynaptic cell membrane causing ion channels to open. A postsynaptic potential is then created between intracellular and extracellular space. These potentials are called field potentials (Speckmann and Caspers, 1979), and they constitute the basic mechanism underlying the potentials recorded by EEG. While action potentials last approximately one millisecond, field potentials can last tens or even hundreds of milliseconds (Luck, 2014). The activity recorded through EEG is thought to be generated mainly by pyramidal cells, which have a perpendicular orientation relative to the cortical surface (Fisch, 1999). When thousands of field potentials occur simultaneously at a similar location and orientation, it is possible for their summated activity to be detected as a voltage difference on the scalp, and it can be recorded using EEG (Lopes da Silva and Van Rotterdam, 2005; Nunez and Silberstein, 2000).

2.2.2 EEG signal acquisition and processing

The EEG technique utilises the measurement and recording of fluctuating field potentials in the brain over time (Kamp et al., 2005). To this end, electrodes are

positioned on the scalp at locations based on the Standardised International 10-20 system, which employs relative distance measurements using internationally recognised anatomical landmarks on the skull (Jasper, 1958; Klem et al., 1999). This standardised electrode placement ensures that the names and positions of electrodes are consistent across different laboratories so that the corresponding EEG recordings can be comparable allowing for meaningful interpretation of findings. For the placement of electrodes, a suitable gel or liquid must be applied in order to facilitate the conduction of signal (Rowan & Tolunsky, 2003).

For all the EEG recordings described in the current thesis, a 129-channel net with sponge electrodes (Electrical Geodesics, Inc.) was used. Figure 2.1 shows a flattened representation of the net and the positions of its electrodes. This high density net allows for full head coverage, including much of the face. A saline solution was used as the conductor medium. The Cz vertex electrode was used as the reference (denoted by 'REF' in Figure 2.1). Recordings were taken at a sampling rate of 1000 Hz. A high-pass filter of 0.01 Hz was used online.

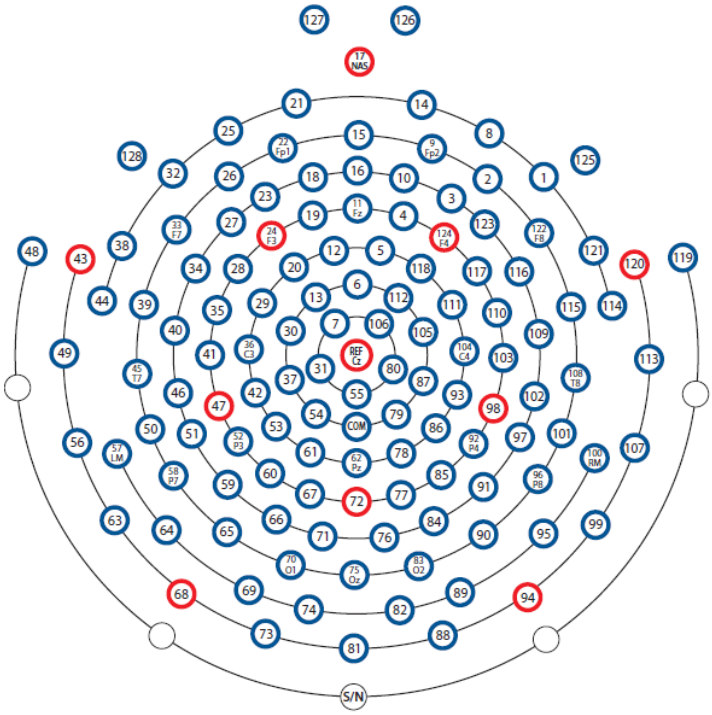


Figure 2.1: Schematic of the 129-channel Geodesics net.

Typically, the adult EEG recording signal ranges between 10 and 100 μV in amplitude (Aurlien et al., 2004). This signal needs to be amplified before it can be measured (Luck, 2014). The resulting amplified signal is subsequently digitised, and the digital recording enables the display and analysis of data. The signal at each specific electrode at a specific time point represents the voltage difference between this electrode and a reference electrode (Luck, 2014). There are different methods that can be used to acquire the reference signal. These include mean recordings from bilateral mastoid electrodes, Laplacian comparison between each electrode and the weighted average of its surrounding electrodes or the common average method which refers to the mean signal of all EEG channels (Nunez et al., 1997). During the EEG recording, low-pass filters can be used to attenuate high frequency signals and high-pass filters to attenuate low frequency potentials (Luck, 2014).

2.2.3 Advantages and limitations of EEG

The most important advantage of using the EEG technique is that it offers excellent temporal resolution which is in the range of milliseconds (Schneider and Strüder, 2012). This allows for an understanding of stimulus processing in real time which can be particularly useful during investigation of cognitive processes that occur quickly in the brain, such as during decision making. Additionally, EEG offers a more direct measure of neuronal activity compared to indirect responses measured through fMRI or positron emission tomography (PET) (Hari et al., 2010). Furthermore, there are practical advantages for the use of EEG in that it is a non-invasive technique, it can be recorded wirelessly allowing for recordings in a wide range of environments, and is relatively inexpensive compared to fMRI, magnetoencephalography (MEG) or PET (Schneider and Strüder, 2012).

The main disadvantage of the EEG technique is that it has a limited spatial resolution compared to fMRI. Because the EEG activity is recorded from scalp electrodes, the original signal needs to pass through several brain layers such as cerebrospinal fluid and the skull (Nunez et al., 1997). Therefore, exact identification of the source of activity is impossible. Even though advanced source localisation methods can be used to approximately identify intracranial sources, these are by default limited and depend on the accuracy of conductivity models and brain templates

used (Schneider and Strüder, 2012). Despite the accuracy of source localisation methods improving with increasing number of electrodes used during recordings (Babiloni et al., 2001; Lantz et al., 2003; Michel et al., 2004), these techniques can be used as source estimates, but with caution as they are not definitive (Luck, 2014).

2.2.4 Artifact rejection

EEG recordings are sensitive to artifacts, which are electrical signals that do not originate from within brain, but, nevertheless, can obscure the brain signals. Given that an amplification of signal is required during EEG recordings, this also leads to amplification of the artifacts which are not relevant for the analysis of the cognitive activity being investigated. These artifacts can include eye blinks (electrooculographic activity, EOG), parallel eye movements (or saccades), electrocardiographic activity (ECG), muscle movements, or accidental electrode sway. Furthermore, external noise from the environment, such as activity from electrical sources or appliances, can induce a 50 Hz wavelength artifact in the EEG signal. The two main problems associated with artifacts are that they can be large compared to the EEG signal of interest, thus, decreasing the signal-to-noise ratio (SNR), and, sometimes, they can occur systematically (e.g., eye blinks) rather than randomly in isolated instances (Luck, 2014). Even though some caution can be taken to reduce external noise, specific types of artifacts, such as eye blinks, cannot be completely eliminated. Therefore, prior to a meaningful interpretation of experimental findings, these artifacts must be eliminated from the EEG recording (Luck, 2014).

The simplest, but also the most time consuming, artifact rejection technique is the visual inspection of individual trials and manual disregarding of trials containing artifacts (Luck, 2014). Additionally, filter application might help with the rejection of artifacts, particularly those that are of a known amplitude. For instance, 50 Hz noise can easily be reduced by applying a ‘notch’ filter (Luck, 2014). Sometimes, it might be the case that only one channel is showing an artifactual pattern consistently throughout the experiment (e.g., because the electrode is broken). Interpolation of this electrode, which entails replacing the original waveform with interpolated values from the surrounding electrode sites, is usually the most suitable strategy in this case. Furthermore, in cases where artifacts have a consistent pattern of activity, such as

those created by eye blinks, principal component analysis (PCA; Berg and Scherg, 1994) or independent component analysis (ICA; Jung et al., 2000) techniques can be used. PCA and ICA do not eliminate entire trials, but rather identify and subsequently separate the average pattern associated with a specific type of artifact and finally subtract the isolated artifactual component from the data (Luck, 2014). Therefore, artifact rejection techniques are a necessary step in the processing of EEG recordings in order to ensure clean data pertaining only to the activity of interest and not to irrelevant extra-cerebral noise.

It needs to be noted, however, that artifact rejection reduces the number of trials, and, consequently, the SNR. Furthermore, participants for whom a large percentage of trials has been rejected (e.g., 25% of trials) usually have to be excluded from subsequent analysis (Luck, 2014). The number of trials that were rejected for each participant and condition is reported in every experimental study presented in the current thesis.

2.2.5 Event-related potentials (ERPs)

ERPs refer to averaged EEG activity that is time-locked to an event or stimulus (Lopes da Silva, 2005). Conventionally, ERP responses to different conditions or stimuli are compared in order to quantitatively analyse EEG data with the underlying assumption that differences in ERP activity are associated with differential processing between conditions (Lopes da Silva, 2005).

Four main steps are typically followed during measurement and quantification of ERPs, namely, the extraction of relevant epochs, baseline correction, averaging, and latency/amplitude measurement (Luck, 2014). Fixed-length segments of data are extracted from the continuous EEG, which are time-locked to the event/stimulus of interest. The exact epoch length depends on the ERP component being measured but, commonly, epochs range between 500-1500 ms following the onset of the stimulus. A pre-stimulus baseline period also needs to be measured for comparison. The baseline period is usually set to be one fourth of the total length of the epoch (typically 100-200 ms), although this can vary depending on the experiment (Luck, 2014). Baseline correction is achieved by subtracting the average pre-stimulus voltage from the waveform. From trial to trial there is variability due to the fact that the EEG is the sum of many different sources of electrical activity in the brain, many of which are not

involved in the processing of the stimulus. However, any brain activity that is consistently elicited by the stimulus is assumed to have approximately the same latency from trial to trial. Thus, by averaging EEG epochs corresponding to each experimental condition from several trials, the component of interest is isolated from the remaining EEG activity. This averaging of event-locked EEG activity to different trials from specific electrodes produces a mean waveform, which has positive and negative voltage deflections that represent different ERP components (Luck, 2014). The ERP waveform becomes more stable as more trials are averaged together. Finally, the two main characteristics of ERP components that are usually compared between conditions are latency and amplitude (Luck, 2014). The two most common ways to quantify the magnitude of a given ERP component are the peak and mean amplitude and latency. The peak method simply uses the largest positive or negative peak voltage observed at a single time point within a given time window. The mean method uses the mean voltage over a specified time window. Furthermore, deviations in latency and/or amplitude of known ERP components can be used to make inferences about a particular function or a specific population (Duncan et al., 2009).

The main advantage of using the ERP technique is the temporal resolution which is given at the range of milliseconds. The main disadvantage is the large number of trials that are required for averaging. This can lead to prolonged experiments, repetitive tasks, and participant fatigue. Nevertheless, the number of trials that are necessary to see robust ERP activity depends on the component of interest, and well established components with a known latency and topographic pattern tend to require less trials (Luck, 2014).

2.2.6 EEG analysis using statistical parametric mapping (SPM)

The main difference between SPM analysis and standard ERP analysis is that SPM employs a whole scalp approach, using data from all electrodes during a selected time epoch. Therefore, SPM constitutes a data-driven clustering approach compared to the classical a priori ERP component analysis (Maris and Oostenveld, 2007). This can be particularly useful when investigating exploratory research questions or when it is difficult to make hypotheses regarding when or where to look for an effect (Kiebel and Friston, 2004; Worsley, 2003). SPM was used to analyse the differences between responses to gains and losses over the entire time epoch after feedback onset and in all

scalp electrodes in the first experiment described in the current thesis, as it represented an initial exploratory investigation.

SPM constitutes a voxel-based approach that employs classical inference to interpret regionally specific responses to experimental factors (Friston et al., 1994; Kiebel and Friston, 2004). Every voxel in the brain is analysed using statistical tests and the resulting statistical parameters create an image called statistical parametric map (Friston et al., 1994). Similarly to three-dimensional space volumes in fMRI analysis, SPM during EEG data analysis uses three-dimensional volumes in which time represents the third dimension. In SPM maps, the value at each voxel represents a statistic that expresses evidence against the null hypothesis (Friston et al., 1994). SPM uses principles of Gaussian random field theory to control for multiple comparisons (Adler, 1981) and degrees of freedom are adjusted for non-sphericity (Kiebel and Friston, 2004). Hence, SPM provides robust control over Type I error while, at the same time, maintains sensitivity for the detection of significant results. The first stage in SPM analysis includes the modelling and standard estimation of ERP effects within subject and trial type, and this can involve observation of multiple ERPs. The second stage models the parameters defined at the first stage among trial type and participants, allowing classical inference (using t- or F-statistics) about experimental effects using contrast vectors (Kiebel and Friston, 2004). SPM analysis offers an unbiased analysis which does not assume that an effect needs to cover the full duration of an ERP component or its peak. As ERP components are usually generated by multiple cortical source dipoles, it is likely that an effect can also occur in areas of the scalp other than the site manifesting the dominant part of the component. In particular, in FRN, which was the main component of interest in the experiments presented in the current thesis, strong components of opposite polarity often co-occur with the activation cluster seen on the vertex. Thus, SPM during an exploratory investigation can reveal more aspects of data compared to the standard ERP analysis which would focus on one selected component.

2.2.7 Source analysis

The ultimate goal of cognitive neuroscience is to discover how brain structure and function give rise to the cognitive processes under investigation. The EEG technique, although limited in spatial resolution compared to imaging techniques such as fMRI, provides the temporal resolution that is essential in order to measure cognitive processes in real time. As such, the goal of EEG source localisation is to provide a measurement of the time course of neural activity in specific brain regions. Topographic maps that represent the configuration of the potential field at a single moment in time can be constructed from EEG recordings. The analysis and interpretation of these topographic maps can provide information about the potential brain sources and direct the next source analysis steps. The underlying concept behind EEG source analysis is to fit sources at all brain regions contributing to the observed topographic maps. Therefore, EEG source localisation entails inferring the active brain source from the observed EEG signal. The resulting source waveforms represent the modelled brain activities and answer the question of if and when activity takes place in a specified brain region.

In general, the source localisation of EEG activity is associated with the 'forward' and 'inverse' problems. The forward problem refers to determining the potential scalp distribution given a number of intracerebral sources. In the forward solution, source locations and orientations represent independent variables and their associated source waveforms constitute the dependent variables. If a single dipole is placed in a conductive sphere, it is relatively simple to estimate the precise distribution of voltage that will be observed on the surface of the sphere. To solve the forward problem, a head model is created that describes the propagation of the volume currents to the scalp and represents the voltage at any electrode due to a current dipole with a given location and orientation. The head model needs to take into account the different electrical conductivity properties of several parts of the head, such as the skull. The volume conduction of the brain results in a widespread scalp topography with a maximum over the activated cortical sheet. A corresponding activity of opposite polarity appears on the other side of the head, so that any negativity has a corresponding positivity at another scalp location and vice versa. The inverse problem refers to the identification of intracerebral sources based on the observed scalp

potential distribution (i.e., what are the sources if the scalp waveforms/topographies are known). However, it is difficult to estimate a unique solution for the inverse problem because a large number and combination of possible source locations can contribute to the observed topographic distribution. In order to find a plausible solution, several assumptions and constraints must be considered in order to reduce the number of potential alternative solutions. The forward problem is an integral part of the inverse problem in that the inverse problem is estimated using the forward solution. In the hypothetical condition where there is only one dipole placed in a conductive sphere with known conductivity properties and there is no noise, the inverse problem can be solved by comparing forward solutions from a model dipole with the observed scalp distribution and then adjusting the dipole to reduce the discrepancy between the predicted and observed distributions. However, no unique solution can be found if the number of sources and their locations are unknown, as in the case of real EEG recordings. In other words, for any given scalp distribution, there is an infinite number of possible sets of dipoles that could produce that specific scalp distribution (Helmholtz, 1853; Plonsey, 1963). Nevertheless, it is possible to reduce the number of possible solutions which consequently reduces the error in source placement and several techniques have been proposed to address this.

The techniques that have been proposed for source analysis of EEG data fall into two main categories: (1) discrete source models and (2) distributed source models. The discrete source approach utilises a small number of equivalent current dipoles (ECDs), each of which represents the activity over a small cortical region (up to 3 cm^3), and assumes that these dipoles vary only in strength over time. Each ECD is represented by its location, orientation and strength. One of the most commonly used discrete source approaches is ECD fitting within Brain Electrical Source Analysis (BESA; MEGIS GmbH, Germany) program. BESA is based on the assumption that the spatiotemporal distribution of voltage can be adequately modelled by a small set of dipoles (less than 20), each of which has a fixed location and orientation but varies in magnitude over time (Scherg and Von Cramon, 1985). Each dipole has six major parameters, three indicating its location, two indicating its orientation, and a magnitude parameter which varies over time. Each dipole is represented by a sphere indicating its location and a short line showing its orientation. Each dipole is also associated with a source waveform which graphically represents the temporal

evolution of the dipole moment, thus, showing how the estimated magnitude for that dipole varies over time.

The first step to create a source model using the BESA ECD fitting approach is to define an initial model by fitting one ECD at a single time point or over a specified time interval. The BESA algorithm fits the ECD by determining the optimum location and orientation in order to explain the data in the specified interval as well as possible. The second step is the re-evaluation of the current model of ECD locations and orientations. BESA calculates the forward model topography for the fitted ECD(s) by computing a magnitude for each dipole at each time point so that the sum of the dipoles yields a scalp distribution that matches the observed distribution as closely as possible for each time point. Next, the predicted model scalp distribution is compared with the observed scalp distribution of voltage resulting from the recorded data. The difference between recorded data and modelled data defines the residual waveforms. The normalized sum of squares over electrodes of this residual activity is the residual variance (RV), that is, the unexplained fraction of the data variance. The goal of the BESA algorithm is to find the set of dipole locations and orientations that provide the optimal fit between the model and the data (the fit that yields the lowest RV). Finally, ECD location and orientation are adjusted until the RV is maximally reduced. That is, on each iteration, the forward solution is calculated, producing a particular RV, and then the locations and orientations of the ECDs are adjusted to try to reduce the RV.

Distributed source models divide the brain into voxels creating a cubic grid spanning the whole brain volume. Such models compute a pattern of activation strengths for these voxels that can explain the observed distribution as well as satisfy additional mathematical constraints. The most important advantage of distributed approaches is that they do not depend on assumptions about the number and location of brain generators. Nevertheless, as distributed source models contain more sources than electrodes, there are many different source current distributions that could produce the observed scalp distribution. Even a coarse segmentation of the brain requires the computation of several different dipole strengths. This non-uniqueness problem is intensified as the brain is divided into smaller voxels. Therefore, constraints need to be defined in order to enable selection of the optimum solution. For instance, it has been proposed to select the one solution that both produces the observed scalp distribution and has the minimum overall source magnitudes (minimum norm

solution; Hämäläinen and Ilmoniemi, 1994). Derivatives of this method include Low Resolution Electromagnetic Tomography (LORETA; Pascual-Marqui et al., 1994), standardised LORETA (sLORETA; Pascual-Marqui, 2002), and Local Auto Regressive Average (LAURA; de Peralta Menendez et al., 2001). The result of the method used is displayed superimposed on the anatomical MR image. Because no individual MRI is available, BESA software implementing these procedures automatically uses a standardised MRI template for this purpose. The main advantage of using distributed source approaches compared with discrete source approaches is that the former are relatively quickly generated and the experimenter does not have to decide on the number of sources and the respective fit intervals. Despite this, all distributed source approaches suffer from smearing and crosstalk causing the reconstructed image to appear blurred and non-focal and, consequently, the reconstructed activity at one source location represents not only brain activity at the modelled location but also from other brain regions. Iterative approaches, such as Classical LORETA Analysis Recursively Applied (CLARA; Hoechstetter et al., 2010) aim to combine advantages from discrete and distributed source images and can help to make distributed images more focal. They iteratively apply distributed source images with a successive shrinking of the source space. The result is more focal than the general distributed methods, decreasing the spread of activity substantially.

Therefore, to directly compare discrete and distributed approaches, in discrete source analysis, each ECD represents an extended brain region and the number of sources is smaller than the number of electrodes. The discrete source model is defined by fitting or seeding, and the result is a multiple source model and source waveforms. If the source model contains all active brain regions, the source waveforms represent their activity, meaning that they separate and mutually contrast their activities with minimum crosstalk. However, because the source model needs to be defined, user interaction is required (e.g., decision on the number of sources, fit intervals). In distributed source analysis, each ECD represents one small brain segment and the number of sources is larger than the number of electrodes. The distributed source model is predefined (along the brain surface or on a regular volume grid), and the result is a 3D volume image, one for each time point. However, the images show smeared, non-focal activity, with substantial crosstalk between sources, and it is difficult to separate activity of brain regions positioned close to each other. Despite

this, because the source model is pre-defined, source images are generated easily and quickly, with minimum user input.

In the current thesis, both a discrete and a distributed source localisation method were employed. The first technique involved source modelling using BESA (i.e., discrete method) by fitting ECDs sequentially in the order of peak latencies of grand average ERPs evaluated using global field power (GFP) waveform. Each ECD was fitted in the time window corresponding to a peak in the GFP waveform. As such, ECDs were fitted consecutively beginning with short latency components. The fitting procedure was stopped if the residual variance was not considerably reduced by adding another source dipole. The second technique employed CLARA (i.e., distributed method) as an independent source localisation method to verify the presence of each ECD fitted using the sequential technique. CLARA is an iterative application of the LORETA algorithm that reduces the source space in each iteration. First, a regularised LORETA is computed. Then, in iterative steps, CLARA smooths the previous image and sets all voxels with amplitudes of less than 10% of the maximum activation to zero, effectively eliminating them from the analysis and from the source space in the following step.

However, as already mentioned, EEG source localisation is limited because, although a unique solution with parameters can be produced, it cannot be determined whether this solution is definitively correct. Nevertheless, approximate reconstruction of intracranial sources for a given EEG signal can be useful if the above limitation is taken into account when interpreting source analysis findings. Importantly, the advantage of the high density EGI system used for the experiments presented in the current thesis is that it offers whole head coverage, which includes electrodes positioned over lower scalp regions and face. This characteristic allows for superior modelling of the head sphere and improved source localisation compared to standard EEG systems, which is essential for identification of deep cortical sources, such as those located in OFC (Luu et al., 2001; Tucker, 1993). Indeed, it has been proposed that the first step for correct source analysis should be the adequate spatial sampling of the scalp potential fields, which necessitates a high number of electrodes (Michel and He, 2011).

2.3 Summary

The experiments presented in the current thesis employed parametric modelling of choices to investigate individual differences in loss aversion. EEG recordings were used in order to investigate ERP responses following the receipt of positive and negative decision outcomes. Given that loss aversion is a cognitive bias occurring only as a small fragment of the decision making process, the temporal resolution of the EEG technique offered an excellent measure to investigate its neural correlates.

Chapter 3

Study 1: Effects of loss aversion on neural responses to losses: an event-related potential study.

This experiment investigated the effects of individual differences in loss aversion on the evaluation of monetary decision outcomes using EEG.

It is published in Biological Psychology (2017), doi: 10.1016/j.biopsycho.2017.04.005. The format has been altered to match the style of the thesis.

3.1 Abstract

Loss aversion is the tendency to prefer avoiding losses over acquiring gains of the same amount. To shed light on the spatio-temporal processes underlying loss aversion, we analysed the associations between individual differences in loss aversion and electrophysiological responses to loss and gain outcomes in a monetary gambling task.

Electroencephalographic feedback-related negativity (FRN) was computed in 29 healthy participants as the difference in electrocortical potentials between losses and gains. Loss aversion was evaluated using non-linear parametric fitting of choices in a separate gambling task.

Loss aversion was associated with FRN amplitude (233-263 ms) at electrodes covering the lower face. Feedback-related potentials were modelled by five equivalent source dipoles. From these dipoles, stronger activity in a source located in the orbitofrontal cortex (OFC) was associated with loss aversion.

The results suggest that loss aversion implemented during risky decision making is related to a valuation process in the OFC, which manifests during learning choice outcomes.

3.2 Introduction

Loss aversion is the tendency to prefer avoiding losses over acquiring gains of the same amount (Kahneman and Tversky, 1979). Loss aversion affects a large range of economic behaviours, such as willingness to part with an object in one's possession (Kahneman et al., 1990), relative sensitivity to price changes (Hardie et al., 1993; Putler, 1992), decision making in a monetary gambling task (Sokol-Hessner et al., 2009; Takahashi et al., 2012; Tom et al., 2007), or the style of playing golf (Pope and Schweitzer, 2011).

In prospect theory of decision making (Kahneman and Tversky, 1979), individual decisions are modelled by two functions, the probability weighting function and the value function. Loss aversion, typically evaluated in tasks involving decision making under risk (Barkley-Levenson et al., 2013; Canessa et al., 2013; Tom et al., 2007; Wright et al., 2012), is defined as a value function that is steeper for losses than for gains of equal size. Similarly, losses are associated with greater autonomic (Sokol-Hessner et al., 2009; Stancak et al., 2015) and cerebral (Sokol-Hessner et al., 2013; Tom et al., 2007) responses in people with high loss aversion compared to people with low loss aversion. Individual levels of loss aversion have been shown to negatively correlate with the presence of norepinephrine transporters in the thalamus (Takahashi et al., 2012). Further, a recent structural magnetic resonance imaging (MRI) study revealed a positive correlation between loss aversion and grey matter volume in amygdala, thalamus and striatum (Canessa et al., 2013).

A loss in a monetary gambling task is a negative feedback. A wealth of electrophysiological data suggests that presenting information about losses compared to gains is associated with a negative deflection in the electrocortical potential, which is superimposed on the subsequent, typically large, positive P300 component (Nieuwenhuis et al., 2004b; Yeung et al., 2005). This negative electrocortical potential, known as feedback-related negativity (FRN), occurs between 200 and 350 ms after feedback presentation (Gehring and Willoughby, 2002; Miltner et al., 1997; Nieuwenhuis et al., 2004a; Walsh and Anderson, 2012) and shows a characteristic scalp potential map with a spatial maximum in the fronto-central midline region of the scalp (Gehring and Willoughby, 2002; Hajcak et al., 2006; Nieuwenhuis et al., 2004b; Walsh and Anderson, 2012; Yeung and Sanfey, 2004). The cortical source of FRN has

been located near or in the anterior cingulate cortex (ACC) (Bellebaum and Daum, 2008; Gehring and Willoughby, 2002; Hewig et al., 2007; Miltner et al., 1997; Potts et al., 2006; Ruchsow et al., 2002). However, the potential fields during the period of FRN appear to have a more complex topography with positive components occupying the bilateral temporal regions of the scalp, suggesting the possibility that multiple cortical sources might be involved (Gehring and Willoughby, 2002). Indeed, several studies have identified additional brain regions contributing to the generation of FRN (for reviews see Hauser et al., 2014; Walsh and Anderson, 2012), such as the PCC (Badgaiyan and Posner, 1998; Cohen and Ranganath, 2007; Müller et al., 2005; Nieuwenhuis et al., 2005c) and the striatum (Martin et al., 2009; Nieuwenhuis et al., 2005c).

In the context of the present study, punishment sensitivity has been shown to be related to the amplitude of FRN (Santesso et al., 2011; Unger et al., 2012). In studies exploring effects of framing, stronger FRN amplitudes were found in prospects framed negatively compared to those framed positively (Ma et al., 2012; Yu and Zhang, 2014). Further, a recent study showed that loss aversion attenuated amplitudes of a posterior positive slow wave during decisions involving low conflict between competing options (Heeren et al., 2016). These studies suggest the possibility of an association between FRN and loss aversion.

The purpose of the present study was to identify the cortical regions and time period when loss aversion modulates the cortical response to losses during the evaluation of choice outcomes. Although loss aversion affects decision making during the period of evaluation of expected utilities of individual prospects, previous studies also found processing of loss outcomes related to loss aversion (Sokol-Hessner et al., 2013; Sokol-Hessner et al., 2009; Stancak et al., 2015). Neural responses to expected (Knutson et al., 2001) and actually perceived (Delgado et al., 2000; May et al., 2004) losses or gains are processed in an overlapping set of regions. Meta-analyses of fMRI studies typically point to ventral striatum, OFC and VMPFC as playing a central role in value-based decision making (Bartra et al., 2013; Clithero and Rangel, 2014). Therefore, we postulated that loss aversion will be associated with the electrophysiological responses to choice outcomes in one or more regions belonging to the brain valuation system (Bartra et al., 2013; Clithero and Rangel, 2014; Lebreton et al., 2009). To identify the brain regions involved in mediating the relationship between loss aversion and FRN, we applied source dipole analysis and analysed the

associations between source dipole waveforms and loss aversion using correlation analysis. To differentiate the effects of sensitivity to losses from sensitivity to risk, a non-linear parametric method was employed to model the individual choices using three parameters: loss aversion, curvature of the value function (i.e., risk attitudes) and choice sensitivity (Sokol-Hessner et al., 2013; Sokol-Hessner et al., 2009; Stancak et al., 2015). Although the primary focus of the present study was on loss aversion, the curvature of the value function was evaluated as well to check the potentially overlapping effects of these two preference parameters. Finally, choice sensitivity served as an estimation of participants' response consistency throughout the experiment.

3.3 Methods

3.3.1 Participants

A total of 31 participants (16 females) completed the study. Two participants were removed from subsequent analyses due to technical issues encountered during EEG recordings. Thus, the final sample included 29 participants (14 females), aged 22.5 ± 3.6 years (mean ± SD), 4 left-handed. The experimental procedures were approved by the Research Ethics Committee of the University of Liverpool. All participants gave written informed consent in accordance with the Declaration of Helsinki.

3.3.2 Procedure

The experiment involved two different tasks. The first one was a monetary gambling task comprising 100 trials. Participants had to select between two prospects with one of them offering a sure zero outcome or sure non-zero gain and the other an uncertain gain or loss of variable amounts. This task was used to assess individual loss aversion levels. Next, participants completed an EEG experiment involving only uncertain monetary gambles followed by presentation of the outcome. The event-related potential (ERP) analysis of the outcome period served to evaluate the

individual FRN potentials. The purpose of the experiment was explained to participants, who were given instructions for the tasks at the beginning of the session.

3.3.2.1 Loss aversion task

The initial monetary gambling task was adapted from previous studies (Sokol-Hessner et al., 2013; Sokol-Hessner et al., 2009; Tom et al., 2007), and in particular from Stancak et al. (2015). Participants received an initial endowment of £20 and were instructed to use it for gambling during the experiment. They were informed that 10% of the difference between their total gains and losses would be added to or subtracted from this £20 endowment and they would receive the remaining amount as a reimbursement for their participation.

The task consisted of a total of 100 trials. In 80 of those trials, participants decided between a gamble and an alternative sure zero outcome. Each gamble consisted of 8 possible gain amounts (£1.0, £2.0, £3.0, £3.5, £4.5, £5.0, £5.5, £6.0) in combination with 10 possible losses. The losses were computed by multiplying each particular gain value with a coefficient from 0.2 to 2.0 in 0.2 steps in all possible permutations (8 gains × 10 losses). The gain and loss amounts used for these 80 gambles are listed in Table 3.1. Potential gains and losses were associated with equal probabilities (i.e., 50%). In additional 20 trials, participants decided between a gain-only gamble and a sure non-zero outcome. Here, the gain-only gambles offered a 50% chance to win a certain gain amount or zero otherwise, whereas the sure alternative was a smaller gain. These 20 gambles are listed in Table 3.2. Trials were presented in random order for each participant.

Participants were seated in front of a 19-inch CRT monitor, and rested their right hand on a computer mouse. The stimuli were presented using Cogent software 2000 (UCL, London, United Kingdom) for Matlab (Mathworks, Inc., USA). The trial structure is shown in Figure 3.1. Each trial began with two possible choices that were displayed on the screen for 4 s. Half of the screen presented a gamble option (e.g., 'You win £3.0, You lose £3.0') in yellow text on black background. Participants were informed that the outcome was always random (i.e., 50% probability). The other half of the screen showed the value of a sure outcome (e.g., £0). Participants were instructed to choose between the two prospects by pressing the left or right mouse button according to the part of the screen they preferred. If the participant selected the

risky gamble option, feedback about the outcome was shown for 1 s ('You won' or 'You lost'). A fixation cross appeared before the start of the next trial that stayed on the screen for 1 s. The duration of this initial gambling task was approximately 15 min.

Table 3.1. Gain and loss amounts used for the 80 mixed gambles.

Gains	Losses									
1.0	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
2.0	0.4	0.8	1.2	1.6	2.0	2.4	2.8	3.2	3.6	4.0
3.0	0.6	1.2	1.8	2.4	3.0	3.6	4.2	4.8	5.4	6.0
3.5	0.7	1.4	2.1	2.8	3.5	4.2	4.9	5.6	6.3	7.0
4.5	0.9	1.8	2.7	3.6	4.5	5.4	6.3	7.2	8.1	9.0
5.0	1.0	2.0	3.0	4.0	5.0	6.0	7.0	8.0	9.0	10.0
5.5	1.1	2.2	3.3	4.4	5.5	6.6	7.7	8.8	9.9	11.0
6.0	1.2	2.4	3.6	4.8	6.0	7.2	8.4	9.6	10.8	12.0

Table 3.2. List of 20 pairs of gain-only gambles and assured non-zero gains.

Pair	Gamble	Sure gain
1	1.0	0.5
2	1.5	0.5
3	2.0	1.0
4	2.5	1.0
5	3.5	1.5
6	4.0	1.5
7	6.0	3.0
8	6.0	2.5
9	6.0	2.0
10	7.5	2.5
11	7.5	3.0
12	9.5	4.0
13	11.0	5.0
14	11.5	5.0
15	12.5	4.5
16	12.5	5.0
17	13.0	5.0
18	13.0	6.0
19	14.0	7.5
20	15.0	6.0

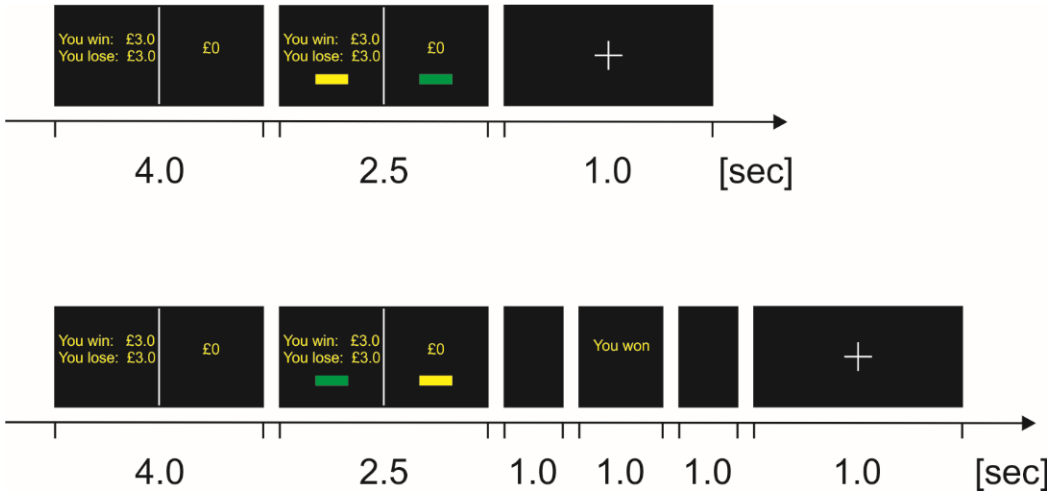


Figure 3.1. Trial structure of the loss aversion task. Top panel: Declined gambles. Each trial began with the presentation of two possible choices, which were displayed on the screen for 4 s. Half of the screen presented a gamble option (e.g., 'You win £3.0, You lose £3.0') with a 50% chance of winning or losing the displayed amount of money. The other half of the screen showed the value of a sure outcome (e.g., £0). Participants were instructed to choose between the two prospects by pressing the left or the right mouse button according to the part of the screen they preferred. If participants chose a sure zero outcome, they would neither lose nor win anything. In the next 2.5 s, the options stayed on the screen and two yellow rectangles appeared at the bottom of the screen. After participants chose their preferred option, the yellow rectangle corresponding to that option turned into green colour to highlight participants' choice. Subsequently, a fixation cross appeared on the screen and the next trial started after 1 s. Bottom panel: Accepted gambles. If participants selected the risky gamble option, a black screen was displayed for 1 s after the 2.5 s response period, and feedback about the gamble outcome was shown for 1 s ('You won' or 'You lost'). A 1 s black screen served as a resting period before the next trial.

3.3.2.2 FRN task

After application of the EEG cap, participants were led into a dimly lit, sound attenuated room and completed the second gambling task. This task was similar to those used in previous studies (Gehring and Willoughby, 2002; Hajcak et al., 2006; Nieuwenhuis et al., 2004b). Figure 3.2 shows the flowchart of the trial procedure. Each trial began with a resting interval during which participants viewed a white cross on a black background. Participants then saw two white rectangles positioned next to each other (one on the left and one on the right side of the screen). After 1 s, the numbers 25 and 5 were presented in either one of the rectangles. These numbers indicated amount of money (in pence) that could be won or lost on that trial. Each number appeared on either the left or right side of the screen and this was counterbalanced across trials. The rectangles never contained the same number on both sides simultaneously. Participants had to choose between these two options by pressing the left or right mouse button. Their chosen option was highlighted for 1 s with a yellow rectangle. Next, the chosen and the alternative outcomes were displayed again with the sign '+' or '-' in front of each number, indicating their valence. The outcome on any trial was randomly generated by the computer and participants had a 50% chance of winning or losing. Thus, the prospects could be either positive or negative numbers but participants could not know this in advance. There were four possible combinations of outcomes (+25 +5, +25 -5, -25 -5, -25 +5). During the outcome period, participants also received feedback about whether their chosen option was better or worse than the other option. The better of the prospects was highlighted with a green rectangle and the worse prospect with a red rectangle. For example, in the case where both numbers were positive (+25 vs. +5), participants won money no matter what they chose. However, winning 25 was still better than winning 5 and, therefore, 25 was highlighted with green. Finally, participants were reminded that the value of each chosen outcome would be added to or subtracted from their initial £20 endowment.

The task consisted of 480 trials, split into 15 blocks of 32 trials. The duration of each block was approximately 5 min. At the end of each block, participants received feedback about the amount of money earned in that block as well as the cumulative amount gained from the beginning of the task.

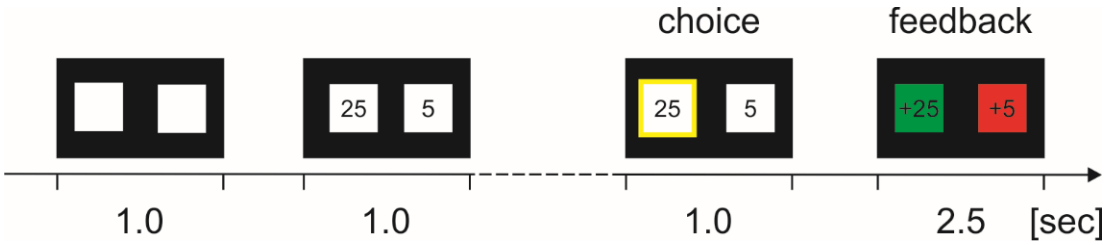


Figure 3.2. Trial structure of the FRN task. Each trial began with the display of two white rectangles positioned next to each other (one on the left and one on the right side of the screen) on a black background. After 1 s, the numbers 25 and 5 were presented in either one of the rectangles. These numbers indicated amount of money (in pence). Participants had to choose between these two options by pressing the left or right mouse button. Their chosen option was highlighted for 1 s with a yellow rectangle. After this, the chosen and the alternative outcomes were displayed with the sign + or – in front of each number, indicating their valence. In addition, participants received feedback about whether their chosen option was better or worse than the unchosen one. The best prospect was highlighted with green colour and the worst with red colour.

3.3.3 EEG Recordings

After completing the loss aversion task, participants were connected to the EEG system. EEG was recorded continuously using a 129-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. This system allows full head electrode coverage as it includes electrodes positioned over lower scalp regions and face, which is essential for identification of deep cortical sources, such as those located in OFC (Luu et al., 2001; Sperli et al., 2006; Tucker, 1993). The sensor net was aligned with respect to three anatomical landmarks; two preauricular points and the nasion. Electrode-to-skin impedances were kept below 50 kΩ and at equal levels across all electrodes, as recommended for the EGI system we used (Ferree et al., 2001; Luu et al., 2003; Picton et al., 2000). The recording band-pass filter was 0.001−200 Hz with sampling rate at 1000 Hz. The electrode Cz served as the reference.

3.3.4 Behavioural analysis

A parametric method was employed to estimate the level of loss aversion using a piecewise function:

$$U(x) = \begin{cases} x^{v+}, & x \geq 0 \\ -\lambda(-x)^{v-}, & x < 0 \end{cases}$$

where v is the curvature of the value function parameter that controls the diminishing sensitivity, x represents the actual outcome from each trial, and λ is the loss aversion coefficient to overstate disutility from losses. Because the whole utility is reference-dependent, outcomes are regarded as gains when $x \geq 0$ or losses when $x < 0$. In line with previous studies (Sokol-Hessner et al., 2009; Tversky and Kahneman, 1992; Wu and Gonzalez, 1996), we employed the assumption of equality of curvature parameters (i.e., $v^+ = v^-$).

The estimation process was based on the logit-function, which gives the probability of acceptance of a risky gamble. Formally, the function can be written as:

$$F(p, x_g, x_l, x_c) = \left(1 + exp\left\{-\mu\left(U(p, x_g, x_l) - U(x_c)\right)\right\}\right)^{-1}$$

where x_g and x_l refer to the monetary amount that participants could win or lose and x_c represents the alternative sure outcome. The probability to win the uncertain gamble is represented by p. In the present study, we employed the common simplification of linear probability weighting (Canessa et al., 2013; Schulreich et al., 2016; Sokol-Hessner et al., 2013; 2009; Tom et al., 2007) and probabilities of gains and losses were equal throughout the experiment at $p = (1 - p) = 0.5$. We further assumed that participants combined their utility and probability in a linear manner, which implies $pU(x) = U(px)$.

The logit parameter μ denotes the sensitivity to utility deviations. A greater μ suggests a greater consistency in applying the respective prospect-theoretic model to individual decision making behaviour. On the other hand, smaller μ indicates more random choice (approaching a random choice with 50:50 probability of acceptance vs. rejection in its extreme.

One hundred choices were collected for each participant. Denote Z_i as the choice related to the gamble i, where Z_i equals one if the participant proceeds with the uncertain gamble, otherwise Z_i will remain zero. The log likelihood function is given by:

$$\sum_{i=1}^{100} Z_i \log\Big(F\big(p, x_g, x_l, x_c\big)\Big) + (1 - Z_i) \log\Big(1 - F\big(p, x_g, x_l, x_c\big)\Big)$$

The values λ, v and μ were obtained by finding a proper set of estimates to maximise the above equation. Since this process involved a non-linear optimisation, a numerical approximation method has been applied using the Nelder-Mead simplex algorithm (Nocedal and Wright, 2006) implemented in Mathematica 9.0 (Wolfram Research, Inc., USA).

3.3.5 EEG analysis

EEG data were pre-processed using BESA software v. 6.0 (MEGIS GmbH, Germany). EEG signals were spatially transformed to reference-free data using common average reference method (Lehmann, 1987). This spatial transformation restored the signal at electrode Cz which was also used in further analyses. Eye blinks and, when necessary, electrocardiographic artifacts were removed by principal component analysis (Berg and Scherg, 1994). Further, data were visually inspected for the presence of any movement or muscle artifacts, and epochs contaminated with artifacts were excluded. The average number of accepted trials in each condition was: loss feedback: 215.97 ± 7.73 (mean ± SD); gain feedback: 217.62 ± 11.10. The average number of trials accepted did not differ across conditions ($p > 0.05$). Data were filtered from 0.5−30 Hz. ERPs in response to outcome were computed separately for each feedback condition (gain or loss) by averaging respective epochs in the intervals ranging from 100 ms before outcome onset to 500 ms after outcome onset. Epochs were baseline corrected using a time window of -100 to 0 ms relative to the onset of feedback.

Data were exported to SPM12 software package (Statistical Parametric Mapping, UCL, England; http://www.fil.ion.ucl.ac.uk/spm/software/spm12). Data from each subject and each outcome condition during the epoch -100 to 500 ms were

converted into three-dimensional scalp-time images. The electrodes were mapped onto a standardised scalp grid sized 32 × 32 pixels (pixel size 4.25 × 5.3 mm^2) representing the field potential planes stacked over the time axis. Images were smoothed with a Gaussian kernel of 9 mm × 9 mm × 20 ms (full width at half maximum).

After calculating the contrast of gain-minus-loss, a multivariate regression analysis was computed with the smoothed scalp-time images of 29 participants as the dependent variable, and loss aversion λ, curvature of the value function v and log-transformed values of choice sensitivity μ as the predictor variables. The T-contrasts representing positive or negative correlations with λ and v were evaluated. An uncorrected p value of 0.001 was used to statistically threshold the data, and significant clusters were only accepted if they were larger than 20 space-time voxels.

3.3.6 Source reconstruction

Grand average potentials comprising both gains and losses were analysed using source dipole analysis in BESA software v. 6.0 (MEGIS GmbH, Germany). Equivalent current dipoles (ECDs) were fitted sequentially in the order of peak latencies of individual ERPs evaluated using global field power waveform, similar to previous studies (Hoechstetter et al., 2001; Stancak et al., 2002; Stancak et al., 2013). Classical low-resolution electromagnetic analysis (LORETA; Pascual-Marqui et al., 1994) recursively applied (CLARA; Hoechstetter et al., 2010) was used as an independent source localisation method to verify the presence of each ECD. In iterative steps, CLARA smooths the previous image and sets to zero all voxels with amplitudes of less than 10% of the maximum activation, effectively eliminating them from the analysis. CLARA analysis employed the singular value decomposition (SVD) regularisation with a cut-off of 0.01% and four iterations. The source activation images covered the whole brain with a voxel size of 7 × 7 × 7 mm^3. If a small difference, in the range of 10 mm, in the location of an ECD and a corresponding CLARA cluster was encountered, the fitted ECD maximum was preferred in order to maintain the integrity of the source dipole model over the entire feedback epoch. A 4-shell ellipsoid head volume conductor model was employed, using the following conductivities (S/m = Siemens per meter): brain = 0.33 S/m; scalp = 0.33 S/m; bone = 0.0042 S/m; cerebrospinal fluid (CSF) = 1.0 S/m.

Approximate Talairach coordinates for each ECD were compared with the Talairach atlas (Talairach and Tournoux, 1988), and the source locations were labelled according to the nearest cortical location.

3.4 Results

3.4.1 Choice parameters

The mean loss aversion λ was 1.05 ± 0.04 (mean ± SEM) and the mean curvature of the value function v was 0.53 ± 0.03. The mean loss aversion value was slightly smaller compared to previous studies (Sokol-Hessner et al., 2009); however, it fitted well with the mean loss aversion of 1.11 in a recent study involving adolescents and adults (Barkley-Levenson et al., 2013). There was no correlation between loss aversion and curvature of the value function ($p > 0.05$). The assumption of a Gaussian distribution was tested using the Shapiro-Wilk test. Both loss aversion ($W(29) = 0.96$, $p = 0.33$) and curvature of the value function had normal distributions ($W(29) = 0.94$, $p = 0.12$). As choice sensitivity μ was not normally distributed ($p < 0.001$), this variable was log-transformed, resulting in a mean value of 2.31 ± 0.26.

3.4.2 FRN

EEG epochs were averaged for each type of outcome (gains and losses), and FRN was quantified by subtracting ERPs to loss trials from ERPs to gain trials (gain-minus-loss difference waveform; Gehring and Willoughby, 2002). Figure 3.3A shows grand averaged waveforms of an averaged EEG potential at electrode Cz at the vertex, and at electrode 38 in the left temporal area for losses and gains. Loss trials (2.73 ± 2.14 μV) resulted in less positive potential amplitudes compared to gain trials (3.30 ± 2.29 μV; $t(28) = 5.49$, $p < 0.001$) during the maximum FRN. Figure 3.3B shows the topographic map of FRN displayed on a volume rendering of a human head. In accordance with previous studies (Gehring and Willoughby, 2002; Nieuwenhuis et al., 2004b), FRN had a positive maximum at central and frontal midline electrodes. However, we also found negative FRN potential components at electrodes overlying

the face, and at lower temporal and parietal electrodes. The presence of multiple negative spatial maxima suggests that more than one cortical source contributed to FRN.

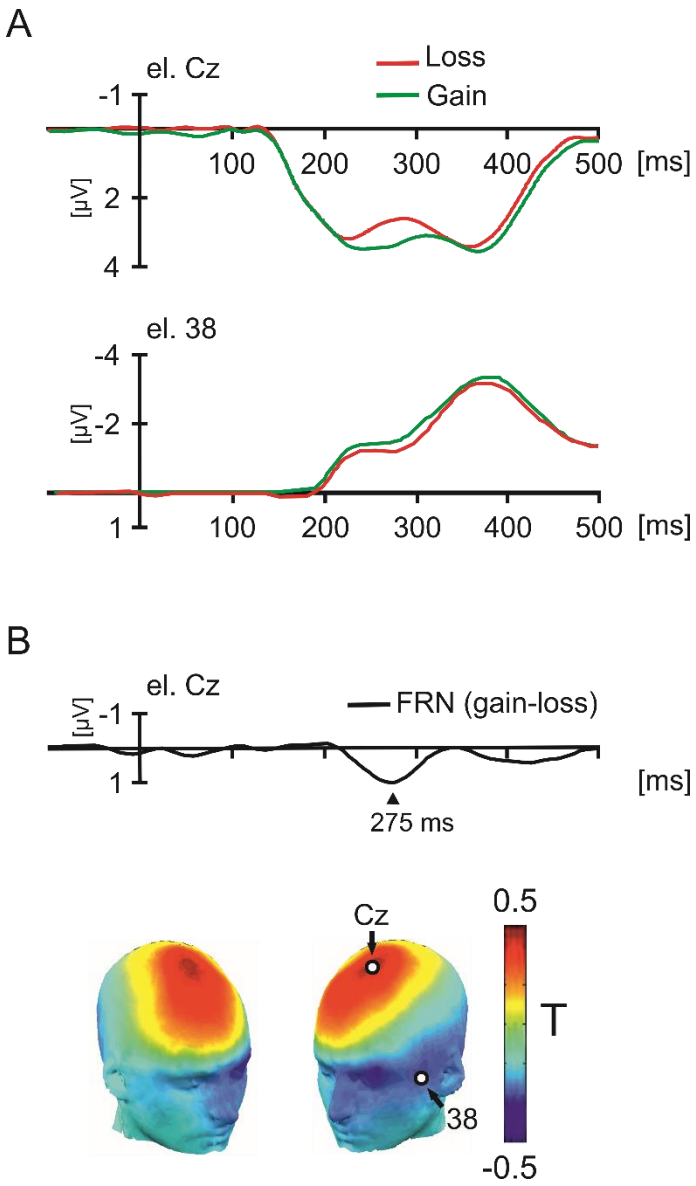


Figure 3.3. A. Grand averaged EEG potentials for gain and loss trials shown at electrode Cz at the vertex, and at electrode 38 in the left temporal area of the scalp. B. FRN is shown as the amplitude difference between gain and loss trials, peaking at 275 ms after feedback presentation (top panel). The scalp topographic map of FRN at its peak (275 ms) latency (bottom panel).

3.4.3 Correlations with loss aversion

A multivariate regression analysis was computed involving the three decision making parameters (λ, v and μ) and the smoothed scalp-time maps for the gain-minus-loss contrast in every time sample ranging from -100 to 500 ms relative to the onset of feedback.

Figure 3.4A shows the scalp-time plot, a standardised scalp map and a volume rendering of the head representing the statistically significant correlation with loss aversion λ. One spatio-temporal cluster operating in the interval 233–263 ms showed a statistically significant negative correlation with λ (uncorrected $p < 0.001$). The temporal maximum of the correlation between FRN and λ had a peak latency of t = 244 ms ($T = 4.64$, $Z = 3.90$, 547 scalp-time voxels). There were no scalp-time voxels showing any statistically significant positive correlations with λ ($p > 0.05$).

To illustrate the correlation between loss aversion and the negative potential during the interval 233–263 ms, the potential value in the scalp-time cluster shown in Figure 3.4A was evaluated in every subject, and correlated with individual loss aversion values. Figure 3.4B shows the scatter plot and the linear regression line between λ and the cluster representing the negative correlation coefficient of $r(28) = -0.91$, $p < 0.001$.

3.4.4 Source reconstruction

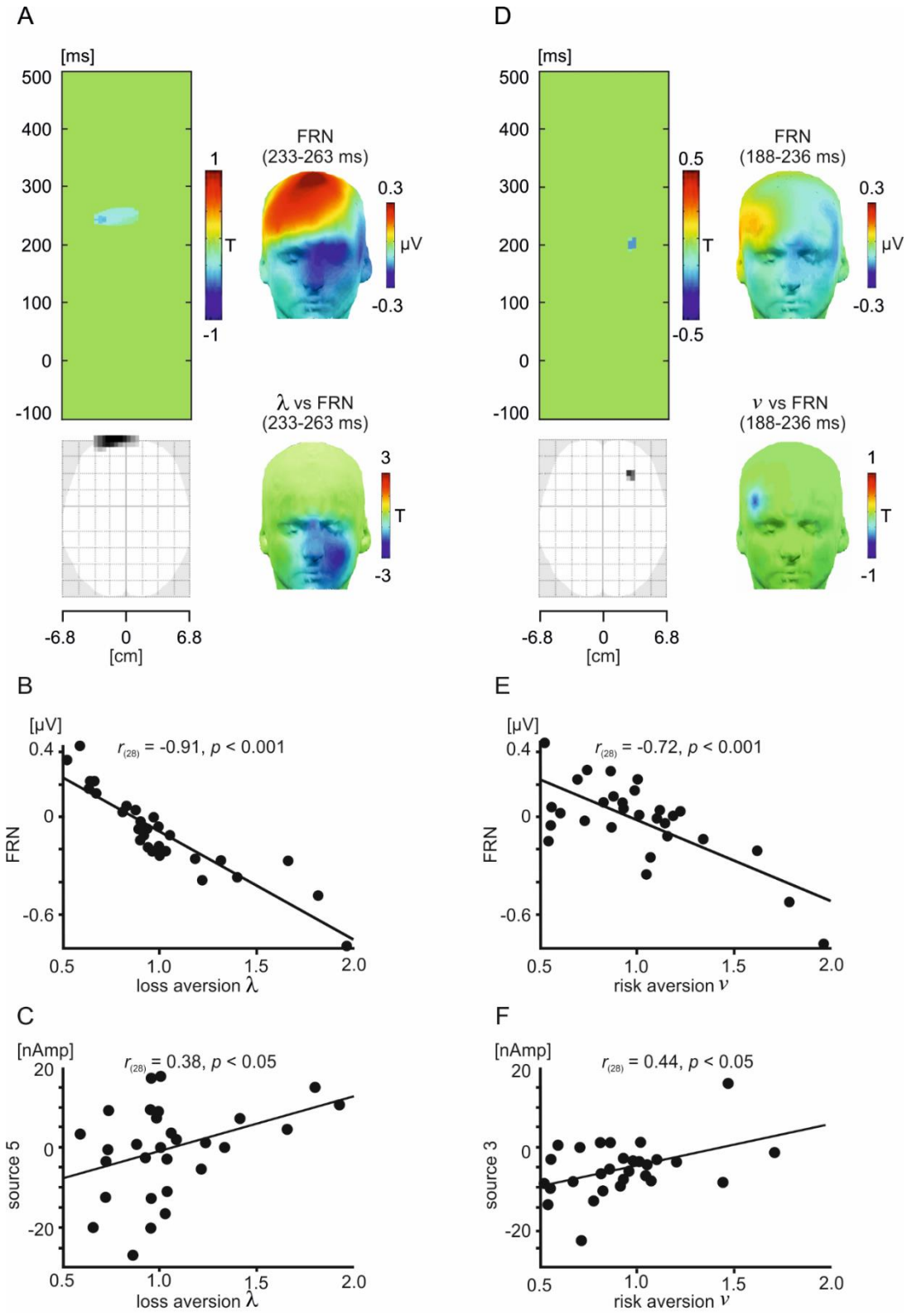
Figure 3.5A shows the grand averaged waveforms and topographic maps of brain activity at different ECDs, on data combined from all the sessions. Figure 3.5B shows locations of the ECDs, which were fitted using global field power waveform, and spatial clusters obtained in the CLARA analysis. The final source dipole model accounted for 94.3% of the total variance, and involved five ECDs.

ECD 1 was located in the PCC (Brodmann area 31; approximate Talairach coordinates: $x = -4$, $y = -24$, $z = 45$ mm) and peaked at 185 ms. ECD 1 had a prevailing radial orientation, related to the positive maximum in the fronto-central electrodes and a negative potential in the lower occipital region of the scalp. ECD 2 was located in the left OFC (Brodmann area 11; approximate Talairach coordinates: $x = -19$, $y = 3$, $z = -5$ mm). This ECD had the negative pole in the left lower facial electrodes and the

positive potential pole at parietal electrodes. ECD 2 peaked at 372 ms. ECD 3 was located in the right medial temporal cortex (Brodmann area 35; x = 27, y = 0, z = -8 mm) and peaked at 388 ms. ECD 3 showed a negative maximum over the occipital electrodes and a positive potential component in the lower frontal region of the scalp. The negative potential over the occipital area of the scalp was located closer to the midline compared to ECD 1, which showed its negative potential component in the right occipital region. ECD 4 was located in the rostral ACC (Brodmann area 32; approximate Talairach coordinates: x = -2, y = 41, z = 8 mm). However, the CLARA cluster also involved the adjacent (VMPFC; Brodmann area 10), suggesting that ECD 4 picked up activation from both these regions. ECD 4 was a radial dipole showing a strong positive potential pole at the vertex region of the scalp. The earliest peak occurred at 180 ms. ECD 5 was located in the OFC (Brodmann area 11; x = 6, y = 7, z = -2 mm). This source showed a double-peak pattern with peak latencies occurring at 227 ms and 380 ms. ECD 5 accounted for a negative potential component in the chin and neck region and a positive component in the posterior parietal region.

The grand average source dipole model was used to quantify the source waveforms of each of five ECDs in two outcome conditions (loss, gain), and every participant. To test the correlations between loss aversion and feedback related potentials in all five sources over the interval showing the statistically significant correlation with loss aversion (233-263 ms), the mean differences between loss and gain ECD waveforms were calculated in the time epoch of 233-263 ms. Loss aversion values were correlated with five ECDs using the Pearson's correlation method. The only statistically significant correlation coefficient surviving the correction for multiple tests was seen in ECD 5 ($r(28) = 0.38$, $p < 0.05$). The scatter plot and the linear regression line representing the positive association between the source activity in the OFC cortex and loss aversion are shown in Figure 3.4C.

The correlations between curvature of the value function v and five ECDs were computed in the interval showing the statistically significant correlation with v in the scalp potential data (188-236 ms). The only statistically significant correlation coefficient remaining after applying the correction for multiple tests was found in ECD 3 ($r(28) = 0.44$, $p < 0.05$). The scatter plot and the linear regression line representing the positive association between the source activity in the right medial temporal cortex and curvature of the value function are shown in Figure 3.4F.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$r_{(28)}$ = -0.91, p < 0.001
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$r_{(28)}$ = 0.44, p < 0.05
source 3
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2.0
risk aversion ν

Figure 3.4. Correlations between FRN and loss aversion and curvature of the value function. A. The vertical green scalp-time plot shows one statistically significant regression between FRN and loss aversion (uncorrected $p < 0.001$). The T values represent the strength and direction of regression over the horizontal axis of the scalp in every time sample from -100 ms to 500 ms. The scalp values over the horizontal axis of the scalp are averages of T values occurring at each vertical point in time for a given horizontal point in the standardised scalp map (from -6.8 cm to +6.8 cm). One interval showed the presence of a statistically significant spatio-temporal cluster. In the interval 233-263 ms, one cluster showed a statistically significant negative correlation between loss aversion and FRN. Below the green panel is the standard scalp map of statistically significant negative regression between loss aversion and FRN. The horizontal axis of the standardised scalp-time map is aligned with the space-time map above. In the right part of this panel, there are two topographic maps. The upper map shows the FRN potential, and the lower map shows the topographic map of the statistically significant regression between loss aversion and FRN in T values. B. The scatter plot and linear regression line representing the correlation between loss aversion and the strength of FRN, $r(28) = -0.91$, $p < 0.001$. C. The scatter plot and linear regression line demonstrating the correlation between loss aversion scores and the strength of ECD 5 located in the right OFC, $r(28) = 0.38$, $p < 0.05$. D. The scalp-time plot of the regression between curvature of the value function and scalp-time maps. In the interval 188-236 ms, one cluster showed a statistically significant negative correlation between curvature of the value function and FRN. The scalp map below the scalp-time plot is the standardised topographic map and shows the topographic location of the cluster showing the statistically significant correlation with curvature of the value function. The two topographic maps in the right part of this panel are the FRN potential map at t = 188-236 ms, and the regression map representing the associations between FRN and curvature of the value function at t = 188-236 ms. E. The scatter plot and linear regression representing the association between curvature of the value function and FRN, $r(28) = -0.72$, $p < 0.001$. F. The correlation between curvature of the value function and source dipole moments in ECD 3, $r(28) = 0.44$, $p < 0.05$.

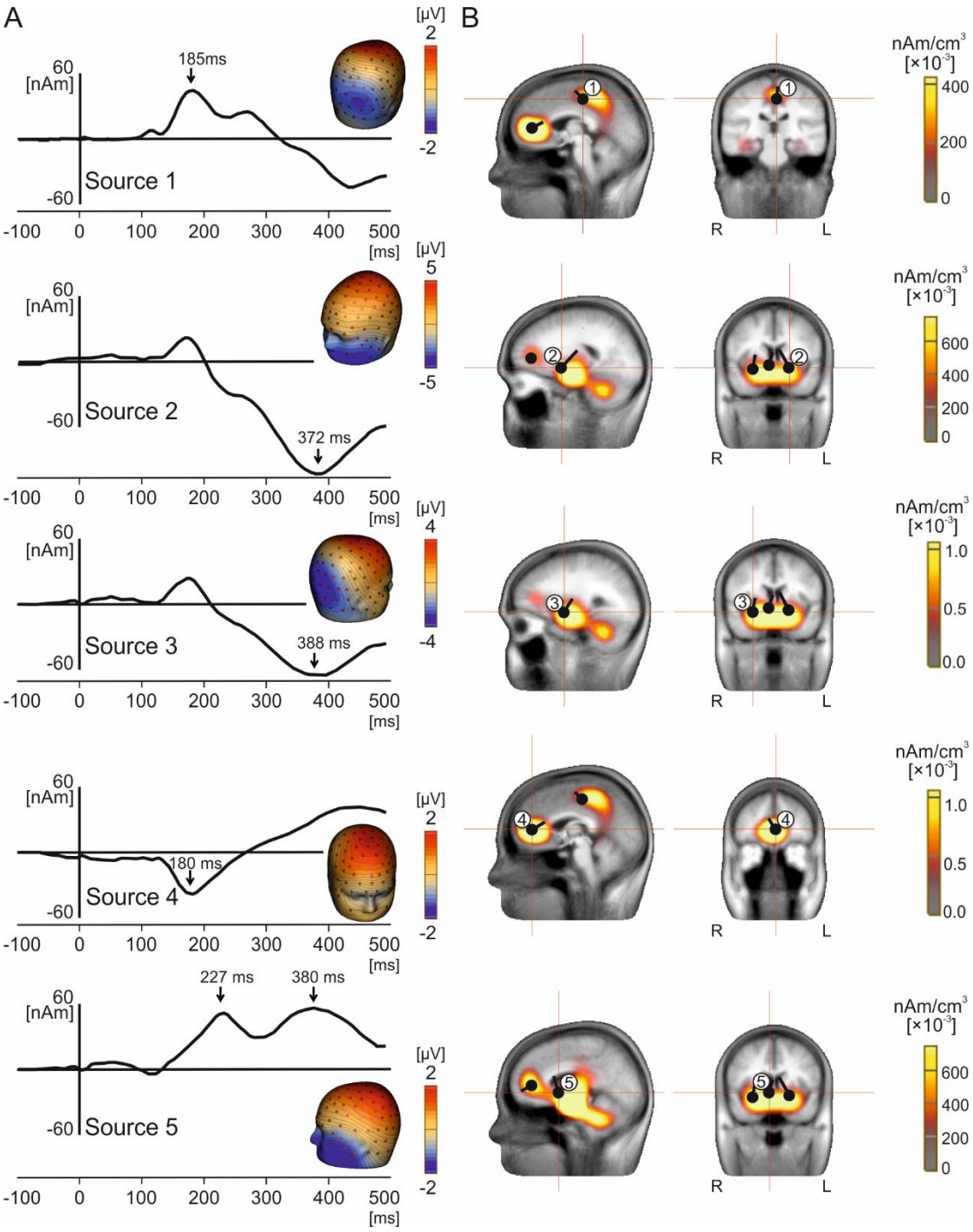

Figure 3.5. Source dipole model and source waveforms underlying ERPs during the outcome period. A. Grand average source waveforms and the topographic scalp maps in five ECDs. Peak latencies are highlighted with arrows. B. Locations of five ECDs in a standard 3-D anatomical MR image and respective CLARA cluster (yellow-orange). Each source is represented by a bar seeded using global field power waveform. The ECDs are associated with numbers, which correspond to the source numbers in (A). L = left, R = right.

3.4.5 Curvature of the value function and FRN

To exclude the possibility that the correlation effects of loss aversion overlapped with effects of the curvature of the value function, we also analysed the correlation between the scalp-time images and curvature of the value function. Figure 3.4D shows the spatio-temporal clusters displaying a statistically significant (p < 0.001) positive or negative correlation with curvature of the value function. The statistically significant associations between curvature of the value function and scalp potentials were seen in one scalp-time cluster located in the right frontal region of the scalp and operating in the interval 188–236 ms. The maximum of the correlations between FRN and v had a peak latency of t = 203 ms (T = 3.75, Z = 3.31, 76 scalp-time voxels). Figure 3.4E shows the scatter plot and the linear regression line between individual curvature of the value function values and the spatio-temporal cluster manifesting a negative correlation ($r(28)$ = -0.72, p < 0.001). Therefore, the data showed that correlations of curvature of the value function and scalp-time maps showed a different scalp topographic location and a different latency epoch to those of loss aversion and scalp-time maps. However, the interpretation value of this correlation is limited, owing to the small amplitude of FRN during the 188–236 ms interval (Figure 3.3A).

3.5 Discussion

The present study analysed the associations between loss aversion and the spatio-temporal activation patterns during the evaluation of decision outcomes in a monetary gambling task using ERPs. Loss aversion was associated with the amplitude of the negative potential part of FRN in a cluster of electrodes covering the lower face (233-263 ms). The correlation between feedback-related potentials and loss aversion was featured in the ECD located in the right OFC. Given that FRN acquired negative signal at the electrodes showing association with loss aversion, the negative correlation corresponds to an increased cortical response to losses in individuals with high levels of loss aversion. The spatio-temporal pattern associated with loss aversion differed from the pattern associated with curvature of the value function; curvature of the value function correlated with FRN in an earlier latency interval (188-236 ms)

when FRN was very weak, and the ECD mediating this correlation was located in the right medial temporal cortex.

3.5.1 FRN and cortical sources

FRN potential, evaluated as the difference waveform between loss and gain trials, was consistent with previous studies both in the peak latency and the fronto-central spatial maximum (Gehring and Willoughby, 2002; Nieuwenhuis et al., 2004b). Our study extends previous research by showing further potential components in the lower facial, temporal, and occipital regions of the scalp, suggesting the presence of more than one dipole. Source localisation of ERPs during the outcome period yielded five cortical sources located in bilateral OFC, rACC/VMPFC, PCC, and the right medial temporal cortex. This finding accords previous studies reporting the generators of FRN in multiple brain regions (Badgaiyan and Posner, 1998; Cohen and Ranganath, 2007; Gehring and Willoughby, 2002; Hewig et al., 2007; Luu et al., 2003; Miltner et al., 1997; Müller et al., 2005; Nieuwenhuis et al., 2005c; Ruchsow et al., 2002; Walsh and Anderson, 2012).

OFC and VMPFC are prominent parts of the brain valuation system, which is employed in outcome processing (Bartra et al., 2013; Clithero and Rangel, 2014), in evaluation of goods in the absence of risky decision making (Elliott et al., 2008; Lebreton et al., 2009) and whilst decisions are made (Chib et al., 2009; Plassmann et al., 2010). However, the three additional cortical regions identified in the source dipole model (PCC, rACC and medial temporal cortex) also play roles in decision making.

PCC has been linked to automatic subjective value computation (Grueschow et al., 2015), comparison between alternative choices (FitzGerald et al., 2009) and reward magnitude (Ballard and Knutson, 2009). Additionally, the peak latency of the source located in PCC corresponded to the P200 component, which has been shown to encode the predictability of outcomes (Polezzi et al., 2008), magnitude of monetary outcomes (San Martín et al., 2013) and outcome history (Osinsky et al., 2012).

Activations in rACC have been associated with emotional processing (Bush et al., 2000), error detection (Kiehl et al., 2000; Menon et al., 2001; Rubia et al., 2003; Ullsperger and von Cramon, 2001) and coding of reward value (Di Pellegrino et al., 2007; Marsh et al., 2007).

As far as the source dipole in medial temporal cortex is concerned, previous studies reported activations associated with negative feedback (Coricelli et al., 2005), reward expectancies (Ramnani et al., 2004) and risk taking (Paulus et al., 2001).

Overall, our results show that processing the outcomes of decisions in a monetary gambling task involves activations of brain regions implicated in assigning values to goods, emotions, reward and punishment, and monitoring outcomes and errors.

3.5.2 Loss aversion and FRN

Loss aversion modulated the amplitude of FRN in the early latency period of 233–263 ms on the ascending limb of FRN peak (275 ms). Due to rigorous statistical thresholding, which was necessary to account for multiple tests, only one small space-time cluster of activation has survived the correction. However, this cluster was part of a strong negative FRN component seen at the whole left lower face (Figure 3.3A). The modulation of FRN in lower facial electrodes suggests that one or more deep cortical sources were involved (Luu et al., 2001; Sperli et al., 2006; Tucker, 1993). Indeed, the negative potential component seen at the face was associated with the ECD in the right OFC, which is where the correlation with loss aversion was found. OFC has been reported to be involved in computing the values of goods (Elliott et al., 2008; Lebreton et al., 2009), encoding reward/punishment magnitude (O'Doherty et al., 2001; Roesch and Olson, 2004; Tremblay and Schultz, 1999) and mediating hedonic experience and evaluation of affective valence of stimuli (Cunningham et al., 2009; Kringelbach et al., 2003). Given the importance of OFC in hedonic evaluation of decision outcomes and the specific relation of loss aversion to outcomes of negative hedonic value, the present data are consistent with the role of OFC in decision making.

Previous studies have shown that processing of positive emotional stimuli are associated with activity in the left hemisphere, whereas processing of negative emotional stimuli are associated with activity in the right hemisphere (Ahern and Schwartz, 1985; Canli et al., 1998; Davidson, 1998; Lane et al., 1997; Lang et al., 1998; Mandal et al., 1991; Tucker, 1981; Windmann et al., 2006). Although the outcome period was associated with activation in bilateral OFC, only the right OFC showed a statistically significant correlation with loss aversion. Given that loss aversion is a response to a negative prospect/outcome (monetary loss), this right-

hemisphere lateralisation in the correlation between OFC and loss aversion is in line with the right-hemisphere prevalence in perception of hedonically negative stimuli (Ahern and Schwartz, 1985; Canli et al., 1998; Davidson, 1998; Lane et al., 1997; Lang et al., 1998; Mandal et al., 1991; Tucker, 1981; Windmann et al., 2006).

The present study adds to previous data showing that individual levels of loss aversion correlated with activations in the VMPFC (Tom et al., 2007), ACC (Canessa et al., 2013), and ventral striatum (Canessa et al., 2013; Tom et al., 2007) during the decision period, and in amygdala during the outcome period (Sokol-Hessner et al., 2013). Our data suggests that OFC provides an individually tuned neural signal about subjective value of loss or gain, and that this signal is associated with the tendency to avoid losses manifested in declining monetary gambles. Further studies should address whether the correlation between the activation in OFC and loss aversion during the outcome period would be also found in ERPs during the decision period.

Although we also found a correlation between the curvature of the value function and the scalp-time maps, the correlation between ERPs and the curvature of the value function in the interval 188-236 ms was not interpreted due to the weak FRN signal in this latency interval. However, the spatial location of the curvature of the value function correlation cluster, the time epoch, and the cortical source displaying a correlation with curvature of the value function differed from loss aversion data. These differences, together with the lack of correlation between loss aversion and curvature of the value function, suggest that the correlation between loss aversion and FRN seen in the present study was not contaminated with curvature of the value function.

To conclude, the individual level of loss aversion is associated with the strength of electrocortical response to decision outcomes. Results suggest that increased neural signals for loss outcomes in the OFC are associated with utility functions that are steeper for losses than gains during decision making under risk. Although the present study shows an association between loss aversion and activation in OFC only during the evaluation of decision outcomes, it is possible that a similar mechanism is also implemented during the evaluation of anticipated outcomes in the course of the decision phase.

Chapter 4

Study 2: Loss aversion is associated with the processing of actual but not counterfactual decision outcomes.

This experiment investigated the association of individual differences in loss aversion with the neural processing of actual and counterfactual decision outcomes.

It is currently under review.

4.1 Abstract

Losses tend to be overvalued compared to gains of the same nominal value, a phenomenon known as loss aversion. Loss aversion has been shown to augment the neural responses to losses while learning the decision outcomes. However, decision outcomes are often evaluated in comparison with foregone outcomes. It is not clear if loss aversion also affects neural responses to counterfactual outcomes such as missed gains or losses. The present study analysed effects of loss aversion on neural responses to monetary outcomes resulting from both chosen and unchosen prospects (actual vs counterfactual outcomes) using electroencephalographic (EEG) recordings. A monetary gambling task and parametric modelling of choices were used to estimate loss aversion. Participants were asked to accept or reject a series of gambles with 50% chance of winning or losing variable amounts of money. Feedback was given about the actual or counterfactual outcome. Event-related potentials (ERPs) time-locked to feedback onset for both actual and counterfactual outcomes were analysed and correlated with loss aversion. Feedback ERPs indicated differences in the neural processing of actual gains compared to actual losses, while no differences were observed between counterfactual gains and counterfactual losses. Critically, loss aversion correlated only with ERPs accompanying actual outcomes. In contrast, there was no association between loss aversion and counterfactual outcome processing. Results suggest that loss aversion is unrelated to the neural processing of unchosen decision outcomes and is implemented only during processing of factual outcomes.

4.2 Introduction

Economic decisions are often influenced by the tendency to overestimate losses compared to gains of the same amount, a phenomenon known as loss aversion (Kahneman and Tversky, 1979). A number of functional magnetic resonance imaging (fMRI) studies show that loss aversion is encoded by brain regions including the striatum (Canessa et al., 2017; Gelskov et al., 2015; Tom et al., 2007), the ventromedial prefrontal cortex (Tom et al., 2007), the amygdala (Canessa et al., 2013; De Martino et al., 2010; Gelskov et al., 2015; Sokol-Hessner et al., 2013) and the insula (Canessa et al., 2017; Markett et al., 2016). Individual differences in loss aversion have recently been linked to dopamine or norepinephrine activity (Sokol-Hessner et al., 2015; Takahashi et al., 2012; Voigt et al., 2015). Further, monetary losses are associated with stronger autonomic arousal responses compared to gains (Sokol-Hessner et al., 2009; Stancak et al., 2015).

Recent electroencephalography (EEG) studies provide further evidence to support associations between individual differences in loss aversion and electrocortical brain activity. Duke et al. (2018) found a correlation between loss aversion and resting state EEG activity which was stronger in the right –compared to the left- hemisphere in central and posterior scalp regions. In a similar vein, Heeren et al. (2016) demonstrated that loss aversion modulated electrocortical potentials during the decision making phase when participants evaluated gamble prospects with small compared to large gain/loss ratios. Furthermore, Kokmotou et al. (2017) showed that loss aversion correlated with feedback-related negativity (FRN), an event-related potential (ERP) component signalling differential neural processing of positive versus negative decision outcomes which manifests as stronger cortical activity for losses compared to gains (Gehring and Willoughby, 2002; Miltner et al., 1997). This correlation occurred early (233-263 ms) during the evaluation of decision outcomes and was reflected in increased OFC activity.

FRN is one of the most extensively studied ERPs in reward processing literature (Hauser et al., 2014; Walsh and Anderson, 2012). It is commonly elicited by experimental paradigms employing forced-choices between two gambles which are followed by presentation of gain or loss feedback (Gehring and Willoughby, 2002; Hajcak et al., 2006; Holroyd et al., 2006; Nieuwenhuis et al., 2004b; Yeung and

Sanfey, 2004). FRN is evaluated as the difference waveform between averaged potentials time-locked to the presentation of gain and loss outcomes (Gehring and Willoughby, 2002). The resulting potential difference has a fronto-central scalp distribution and its maximum amplitude occurs between 200-350 ms after feedback presentation (Walsh and Anderson, 2012), with the anterior cingulate cortex (ACC) identified as its most likely cortical source (Gehring and Willoughby, 2002; Miltner et al., 1997; Ruchsow et al., 2002; Zhou et al., 2010).

In addition to FRN, another ERP component playing important role in outcome evaluation is the P300; a positive shift in the electrocortical potential occurring approximately 300-500 ms after stimulus onset and acquiring its maximum amplitude at parietal scalp locations (Polich, 2007, 2012). P300 is associated with information processing and attentional mechanisms (Donchin et al., 1978; Polich, 2007). In the context of value-based decision making, it has been suggested to encode reward magnitude (Bellebaum et al., 2010b; Gu et al., 2011; Sato et al., 2005; Yeung and Sanfey, 2004) and reward valence (Bellebaum et al., 2010a; Hajcak et al., 2005; Li et al., 2010; Wu and Zhou, 2009).

Complete evaluation of decision outcomes often depends on counterfactual thinking; the comparison of the actual outcome obtained with alternative possible outcomes which were forgone (Roese and Epstude, 2017). Engagement in counterfactual thinking is emotionally charged and can alter behaviour by influencing subsequent decisions (Zeelenberg, 1999). For example, in the context of decisions involving monetary consequences, previous fMRI studies have demonstrated that missed gains are perceived as losses and lead to emotions of regret or disappointment (Camille et al., 2004; Coricelli et al., 2005). These forgone gains activated the OFC, the ACC and the amygdala (Camille et al., 2004; Coricelli et al., 2005), suggesting an overlap with regions associated with loss aversion.

Despite the evidence provided by fMRI studies on counterfactual thinking, the spatio-temporal aspects of counterfactual outcome processing are less clear as EEG studies provide mixed results. Regarding the role of FRN in counterfactual thinking, forgone gains have been shown to produce more negative ERPs compared to losses, leading to an opposite-valence FRN (Gu et al., 2011; Yu and Zhou, 2009). In contrast, Osinsky et al. (2014) showed that both chosen and unchosen outcomes are processed

similarly, with the classic FRN component being present irrespective of whether outcomes have an actual economic impact for an individual. However, other studies found no evidence for such a differentiation between counterfactual outcomes, suggesting that counterfactual gains and losses lead to amplitudes of comparable strength (Marciano et al., 2018; Yeung and Sanfey, 2004; Yu and Zhou, 2009). Regarding the role of the P300 component in counterfactual outcome processing, results do not support strong conclusions either. Some researchers suggest that there are amplitude differences between counterfactual gains and losses (Marciano et al., 2018; Osinsky et al., 2014; Yeung and Sanfey, 2004; Yu and Zhou, 2009), whereas others propose that both outcomes are evaluated similarly (Gu et al., 2011).

Importantly, the process of counterfactual thinking can be sensitive to individual differences associated with pursuing of rewards, such as being a maximizer versus a satisficer (Jasper et al., 2008; Roese and Olson, 1993). However, to the best of our knowledge, no EEG studies have investigated the influence of such individual differences on counterfactual ERPs. Crucially, counterfactual thinking is enhanced following negative events in general (Roese and Epstude, 2017), and following losses compared to gains in particular (Petrocelli and Harris, 2011). Therefore, we postulated that individual differences in overestimating losses compared to gains –namely, loss aversion- might influence the neural processing of unchosen options. Specifically, we expected that loss averse participants would show increased cortical activations for unchosen gains compared to unchosen losses, as these foregone gains could be counterfactually evaluated as losses. Crucially, the EEG technique offers a temporal resolution in the range of milliseconds, which could help to further disentangle the temporal dynamics of the various underlying fast and automatic processes occurring during decision making. This would be particularly helpful when investigating a cognitive bias, such as loss aversion, which only appears as a small part of the decision making process. Loss aversion can occur during the evaluation of the alternative options and before the outcome of the selected option has been received. Irrespective of whether loss aversion will have a small or large effect on the decision made and the subsequent evaluation of the decision outcome, it will still only be relevant when the decision is being made or when individual differences in loss aversion are to be compared to individual differences in neural responses to outcomes.

The aim of the present study was to investigate the effects of loss aversion on feedback electrocortical potentials for both chosen and unchosen outcomes. A gambling task was used to capture subtle individual differences in decision making aspects (Sokol-Hessner et al., 2013; 2009; Stancak et al., 2015; Tom et al., 2007), during which participants freely decided whether they wanted to accept or reject a series of gambles. ERP responses to gains and losses were analysed separately for accepted and rejected gambles and correlated with loss aversion.

4.3 Methods

4.3.1 Participants

Thirty healthy participants (16 females) completed the study. Three participants were excluded from the analysis as outliers due to extremely low values of loss aversion (< 3 SDs from the mean), similarly to previous studies (Sokol-Hessner et al., 2009). Importantly, inclusion of the outliers did not change the results and, thus, we hereafter report results without them. Therefore, the final sample included 27 participants (15 females), 3 left-handed, aged 21.44 ± 4.07 years (mean ± SD). The study was approved by the Research Ethics Committee of the University of Liverpool. All participants gave written informed consent in accordance with the Declaration of Helsinki.

4.3.2 Procedure

The monetary gambling task used was adjusted from previous loss aversion studies (Kokmotou et al., 2017; Sokol-Hessner et al., 2013; 2009; Stancak et al., 2015). The exact gamble amounts used, stimuli presentation and participants' reimbursement were identical to those described in detail previously (Kokmotou et al., 2017). Participants were rewarded in the way described in Chapter 3. Specifically, they were endowed with an initial amount of £20 and were instructed to use it for gambling throughout the experiment. Similar to the experimental procedures from Chapter 3, it was explained to participants that 10% of the difference between their total gains and

losses would be added to or subtracted from this £20 endowment and they would receive the remaining amount as a reimbursement for their participation in the experiment. As such, it was further explained to participants that their final payment was based on their performance and gambling decisions during the experiment. In short, participants were required to choose between a gamble and a sure outcome. The gamble offered 50% chance of winning or losing variable amounts of money. The alternative sure outcome was either zero or an amount smaller than the potential gain from the corresponding gamble in a particular trial. Participants made a total of 300 choices, split into 3 blocks of 100 trials each. Within each block, 80 trials consisted of choosing between a mixed-gamble (e.g., 'You win £3, You lose £3') and a sure zero outcome. The remaining 20 trials consisted of a gain-only gamble (e.g., 'You win £3, You lose £0') versus a sure non-zero outcome (e.g., £2). The inclusion of both mixed- and gain-only gambles allows for a dissociation of loss aversion (i.e., the steepness of the value function) from risk aversion (i.e., the curvature of the value function); mixed-gambles assess loss aversion while gain-only gambles assess risk aversion (Sokol-Hessner et al., 2013; 2009). The reason is that in the gain-only trials there is no loss to be evaluated so if these are rejected it is because of risk aversion. However, loss aversion is relevant when a loss is possible, as in the mixed-gamble trials. As such, the gain-only trials serve as an estimation of risk aversion when loss aversion is by default excluded because it is not possible to lose. Instead, the potential outcomes of these gain-only gambles are whether the participant will receive something or nothing. Similarly to previous studies (Sokol-Hessner et al., 2013; 2009), only mixed-gamble trials were included in ERP analysis to avoid potential confounding effects of gain-only trials which primarily elicited risk aversion. It needs to be noted that the task and stimuli differed to those described in Chapter 3. Here, both loss aversion and FRN can be elicited and measured through the same task because EEG was also recorded during the loss aversion task. In contrast, loss aversion could not be evaluated simultaneously with FRN in the previous experiment because, during the FRN task, participants did not know in advance which option could result in a win or loss.

If participants accepted the gamble, feedback was given about whether they won (Actual Gain) or lost (Actual Loss) at that trial. If participants rejected the gamble, feedback was given about whether they would have won (Counterfactual Gain) or lost (Counterfactual Loss), if they had chosen to accept it. In both actual and counterfactual conditions, feedback constituted of the monetary amount in green colour with a '+'

sign and red colour with a '-' sign for gains and losses, respectively. Actual feedback was presented on white background while counterfactual feedback on grey background, counterbalanced across participants. Figure 4.1 shows the trial structure.

Parametric modelling of participants' choices based on prospect theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992) was used to quantify decision making style. Probabilities of gains and losses were kept equal throughout the experiment (p = 0.5). The value and logit functions as well as the numerical approximation method used have been described in detail in Chapter 3 (section 3.3.4). Although the same behavioural analysis as described in Chapter 3 was conducted by evaluating loss aversion, risk aversion and choice sensitivity (reported in section 4.4.1), only loss aversion was the focus of this experiment. Further methodological reasons do not allow for a robust association of risk aversion with brain data because these are noisy due to the small number of trials available for risk aversion (approximately 80% less than the loss aversion trials) when using the task described in the previous paragraphs.

4.3.3 EEG Recordings

EEG was recorded continuously throughout the experiment using a 129-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. The sensor net was aligned with respect to three anatomical landmarks; two preauricular points and the nasion. Electrode-to-skin impedances were kept below 50 kΩ, as recommended for this system (Ferree et al., 2001; Picton et al., 2000). The recording band-pass filter was 0.01−200 Hz, the sampling rate was 1000 Hz, and the electrode Cz was used as the reference.

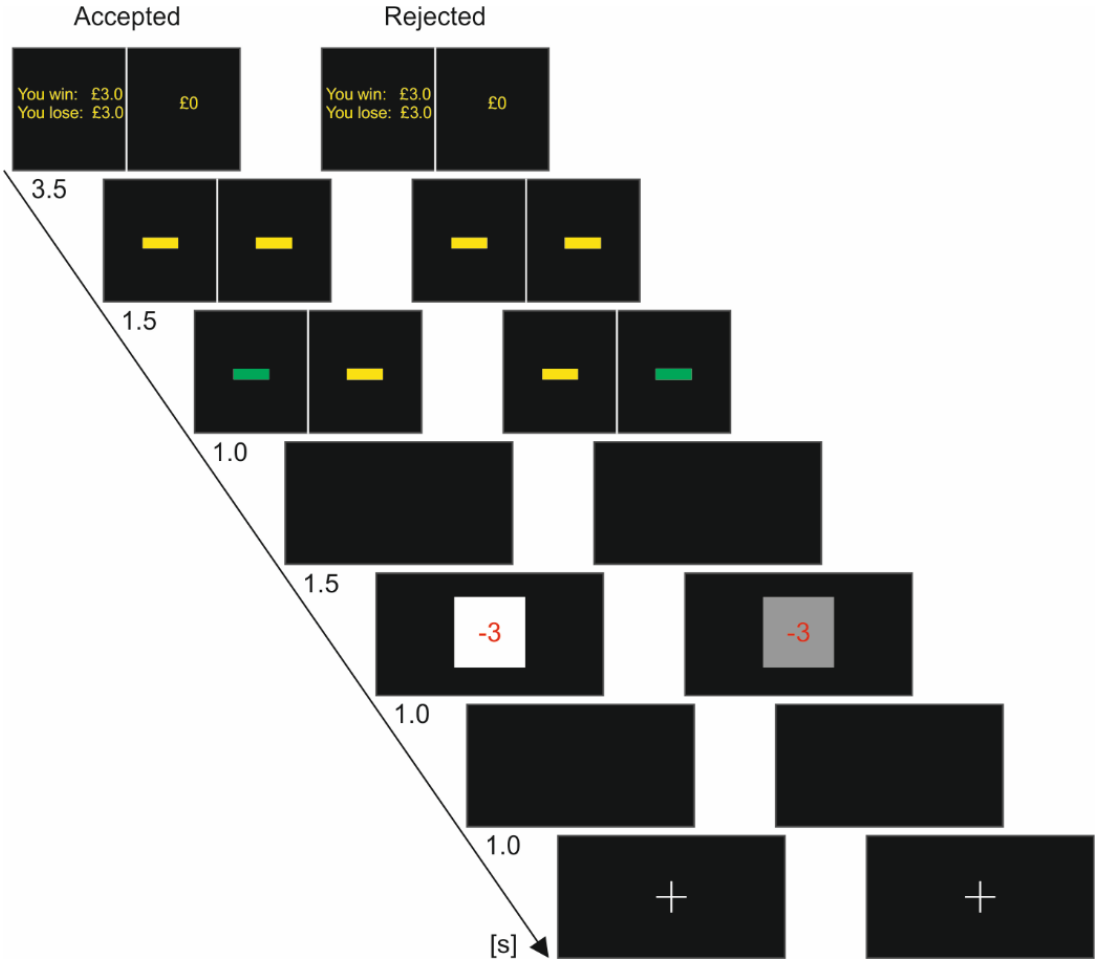

Figure 4.1. Trial structure of the loss aversion task. Left panel: Accepted gambles. Right panel: Rejected gambles. Each trial began with the presentation of two prospects, which stayed on the screen for 3.5 s. Half of the screen presented a gamble option offering 50% chance of winning or losing the displayed amount of money (e.g., 'You win £3.0, You lose £3.0'). The other half of the screen presented a sure outcome (e.g., £0). Subsequently, each of the prospects was replaced by a yellow rectangle. Participants had 1.5 s to select the rectangle corresponding to the option they preferred by pressing the left or right mouse button. Their chosen rectangle turned green for 1 s to highlight their choice and was followed by a 1.5 s black screen. Subsequently, feedback was given about the gamble outcome. This feedback constituted of the monetary amount in green colour with a '+' sign or red colour with a '-' sign for gains and losses, respectively, and stayed on the screen for 1 s. Actual feedback was presented on a white background, whereas counterfactual feedback on a grey background. A 1 s black screen followed the feedback and a fixation cross was presented before the start of the next trial.

4.3.4 ERP analysis

EEG data were pre-processed using BESA v. 6.1 program (MEGIS GmbH, Germany). EEG signals were spatially transformed to reference-free data using the common average reference method (Lehmann, 1987). This spatial-transformation restored the signal at electrode Cz, which was included in subsequent analyses. Eye blinks and, when necessary, electrocardiographic artifacts were removed by principal component analysis (Berg and Scherg, 1994). Data were also visually inspected for the presence of any electrode artifacts due to muscle movement, and epochs contaminated with artifacts were excluded. Data were filtered from 0.5−35 Hz.

ERPs time-locked to feedback onset were computed for each of the four possible outcome conditions resulting from the mixed-gamble trials: participant accepted the gamble and a) won (Actual Gain) or b) lost (Actual Loss) or participant rejected the gamble, but would have c) won (Counterfactual Gain) or d) lost (Counterfactual Loss). Respective epochs in the interval ranging from 300 ms before outcome onset to 1000 ms after outcome onset were averaged. Epochs were baseline corrected using a time window of -300 to 0 ms relative to the onset of feedback. FRN was measured as the mean amplitude pooled over three fronto-central midline electrodes (Fz, FCz, Cz) over a time interval from 250 to 350 ms after feedback onset. P300 was measured as the mean amplitude pooled over three centro-parietal midline electrodes (CPz, Pz, POz) over a time interval from 350 to 450 ms after feedback onset. It needs to be noted that the EEG analysis reported here differed to the one described in Chapter 3. This is because for the previous experiment, which was an exploratory one, data were analysed using SPM, which is a whole-brain method to analyse EEG and for which no electrodes need to be selected a priori. However, since this study is focusing specifically on FRN, electrodes used previously in other studies can now be selected (e.g., Gu et al., 2011; Yu and Zhou, 2009; Marciano et al., 2018; Osinsky et al., 2014).

The average number of artifact-free trials in each condition was: actual gains: 50.0 ± 18.4 (mean ± SD), actual losses: 53.3 ± 20.3, counterfactual gains: 90.3 ± 16.7, and counterfactual losses: 86.7 ± 16.7. As participants on average rejected more gambles than they accepted (see 4.4.1), this resulted in a larger number of counterfactual compared to actual outcomes trials. However, within accept/reject

condition, there were no differences in the number of artifact-free trials for gains versus losses included in the analysis (*ps* > 0.05).

The statistical significance level was set at 0.05 for all analyses and Greenhouse-Geisser correction was implemented for ANOVAs whenever necessary.

4.4 Results

4.4.1 Behavioural results

Mean loss aversion was 1.26 ± 0.04 (mean ± SEM). The assumption of a Gaussian distribution was tested using the Shapiro-Wilk test, which showed that loss aversion had normal distribution ($W(27) = 0.97$, $p = 0.53$). Following the behavioural analysis described in Chapter 3, risk aversion and choice sensitivity were also estimated. Mean risk aversion was 0.37 ± 0.03 and mean choice sensitivity was 2.19 ± 0.28. Both risk aversion and choice sensitivity had normal distributions (risk aversion: $W(27) = 0.94$, $p = 0.09$; choice sensitivity: $W(27) = 0.94$, $p = 0.09$). Furthermore, there was no correlation between loss aversion and curvature of the value function ($p > 0.05$).

On average, participants rejected more gambles than they accepted (rejected: 191.56 ± 7.36 vs accepted: 108.44 ± 7.36; $t(26) = -5.64$, $p < 0.001$), and were faster to reject than to accept gambles (rejected: 0.42 ± 0.01 s vs accepted: 0.50 ± 0.02 s; $t(26) = 2.32$, $p < 0.05$).

4.4.2 ERP results

FRN: Figure 4.2A shows the grand averaged ERP waveforms for the four possible feedback conditions (AG = Actual Gain, AL = Actual Loss, CG = Counterfactual Gain, CL = Counterfactual Loss) pooled over the FRN electrode cluster (Fz, FCz, Cz). The grey shaded area indicates the time window used for statistical analysis (250-350 ms). The two topographic maps represent the amplitude difference between loss minus

gain trials for actual (Actual FRN) and counterfactual outcomes (Counterfactual FRN). The FRN component can be seen only for the actual outcomes condition (Actual FRN). This FRN component showed a negative maximum in central-midline and frontal-midline electrodes and peaked approximately 300 ms after outcome presentation.

To investigate the effects of decision and outcome on FRN, mean ERP amplitude data during 250-350 ms after feedback onset from the FRN electrode cluster (Fz, FCz, Cz) were entered into a 2 (decision: accept vs reject) by 2 (outcome: gain vs loss) repeated measures ANOVA. The time window (i.e., 250-350 ms) selected for statistical analysis was based on previous FRN research (e.g., Yeung and Willoughby, 2002; Walsh and Anderson, 2012) and particularly research exploring counterfactual FRN (e.g., Gu et al., 2011; Marciano et al., 2018; Osinsky et al., 2014; Yu and Zhou, 2009). Furthermore, it was selected based on our own data with the goal of choosing a time window where the differences between conditions were maximum, similar to previous studies (Yu and Zhou, 2009).

The interaction between decision and outcome was significant ($F(1,26) = 6.59$, $p < 0.05$). Paired samples t-tests showed that ERPs following actual losses had more negative amplitudes compared to actual gains (actual losses: 2.91 ± 0.54 μV vs actual gains: 3.70 ± 0.52 μV; $t(26) = 2.32$, $p < 0.05$), while there was no difference in amplitudes between counterfactual gains and counterfactual losses ($p > 0.05$). The main effect of decision was significant ($F(1,26) = 11.58$, $p < 0.05$). Accepted gambles yielded more positive amplitudes compared to rejected gambles (accepted: 3.31 ± 0.50 μV vs rejected: 2.26 ± 0.38 μV). The main effect of outcome was not significant ($p > 0.05$).

Importantly, results were not dependent upon the specific time window selected and, for comparison purposes, we also analysed the data using different time intervals. Specifically, data were further analysed using the peak of the FRN averaged waveform (300-310 ms) and during the statistically significant time window (292-314 ms) obtained by using a permutation analysis (Maris and Oostenveld, 2007) with 5000 permutations in EEGLAB v.12 (Delorme and Makeig, 2004).

FRN 300-310 ms: The interaction between decision and outcome was significant ($F(1,26) = 9.63$, $p < 0.05$). Paired samples t-tests showed that ERPs

following actual losses had more negative amplitudes compared to actual gains (actual losses: 3.06 ± 0.56 μV vs actual gains: 4.12 ± 0.56 μV; $t(26) = 2.65$, $p < 0.05$), while there was no difference in amplitudes between counterfactual gains and counterfactual losses ($t(26) = -1.65$, $p = 0.11$). The main effect of decision was significant ($F(1,26) = 15.77$, $p < 0.001$). Accepted gambles yielded more positive amplitudes compared to rejected gambles (accepted: 3.59 ± 0.52 μV vs rejected: 2.32 ± 0.39 μV). The main effect of outcome was not significant ($F(1,26) = 3.09$, $p = 0.09$).

FRN 292-314 ms: The interaction between decision and outcome was significant ($F(1,26) = 9.61$, $p = 0.005$). Paired samples t-tests showed that ERPs following actual losses had more negative amplitudes compared to actual gains (actual losses: 3.01 ± 0.55 μV vs actual gains: 4.05 ± 0.56 μV; $t(26) = 2.64$, $p = 0.01$), while there was no difference in amplitudes between counterfactual gains and counterfactual losses ($t(26) = -1.58$, $p = 0.13$). The main effect of decision was significant ($F(1,26) = 14.54$, $p = 0.001$). Accepted gambles yielded more positive amplitudes compared to rejected gambles (accepted: 3.53 ± 0.52 μV vs rejected: 2.29 ± 0.39 μV). The main effect of outcome was not significant ($F(1,26) = 3.11$, $p = 0.07$).

P300: Figure 4.2B shows grand averaged ERP waveforms for the four possible feedback conditions pooled over the P300 electrode cluster (CPz, Pz, POz). The grey shaded area indicates the time window used for statistical analysis (350-450 ms). The topographic maps represent the amplitude difference between gain minus loss trials for actual (Actual P300) and counterfactual (Counterfactual P300) outcomes. A P300 component differentiating between gains and losses occurred only for actual outcomes. This P300 component had a positive maximum over parietal-midline electrodes and peaked approximately 400 ms after feedback presentation.

To investigate the effects of decision and outcome on P300, mean ERP amplitude data during 350-450 ms after feedback onset from the P300 electrode cluster (CPz, Pz, POz) were entered into a 2 (decision: accept vs reject) by 2 (outcome: gain vs loss) repeated measures ANOVA. The interaction between decision and outcome was significant ($F(1,26) = 28.30$, $p < 0.001$). Paired samples t-tests showed that actual gains yielded more positive amplitudes compared to actual losses (actual gains: 6.04 ± 0.58 μV vs actual losses: 4.92 ± 0.55 μV; $t(26) = 5.94$, $p < 0.001$), while there was

no difference in amplitudes between counterfactual gains and counterfactual losses ($p > 0.05$). The main effect of decision was significant ($F(1,26) = 17.75$, $p < 0.001$). ERP amplitudes were more positive following accepted compared to rejected gambles (accepted: 5.48 ± 0.56 μV vs rejected: 4.20 ± 0.50 μV). The main effect of outcome was also significant ($F(1,26) = 14.55$, $p < 0.05$), with gains yielding more positive amplitudes compared to losses (gains: 5.10 ± 0.50 μV vs losses: 4.58 ± 0.51 μV).

Similar to the FRN analysis, different time windows were analysed in order to ensure that results were independent of the specific time intervals selected. Again, the peak (390-400 ms) of the P300 averaged waveform and the statistically significant time window (367-429 ms) obtained using a permutation analysis were analysed.

P300 390-400: The interaction between decision and outcome was significant ($F(1,26) = 42.67$, $p < 0.05$). Paired samples t-tests showed that ERPs following actual losses had more negative amplitudes compared to actual gains (actual losses: 4.80 ± 0.66 μV vs actual gains: 6.30 ± 0.62 μV; $t(26) = 6.38$, $p < 0.05$), while there was no difference in amplitudes between counterfactual gains and counterfactual losses ($t(26) = -0.74$, $p = 0.47$). The main effect of decision was significant ($F(1,26) = 15.61$, $p < 0.001$). Accepted gambles yielded more positive amplitudes compared to rejected gambles (accepted: 5.55 ± 0.58 μV vs rejected: 4.16 ± 0.49 μV). The main effect of outcome was significant ($F(1,26) = 17.72$, $p = 0.001$), with gains yielding more positive amplitudes compared to losses (gains: 5.20 ± 0.52 μV vs losses: 4.51 ± 0.50 μV).

P300 367-429: The interaction between decision and outcome was significant ($F(1,26) = 34.75$, $p < 0.001$). Paired samples t-tests showed that ERPs following actual losses had more negative amplitudes compared to actual gains (actual losses: 4.90 ± 0.55 μV vs actual gains: 6.18 ± 0.60 μV; $t(26) = 6.10$, $p < 0.001$), while there was no difference in amplitudes between counterfactual gains and counterfactual losses ($t(26) = -0.65$, $p = 0.52$). The main effect of decision was significant ($F(1,26) = 17.30$, $p = 0.001$). Accepted gambles yielded more positive amplitudes compared to rejected gambles (accepted: 5.52 ± 0.56 μV vs rejected: 4.17 ± 0.49 μV). The main effect of outcome was significant ($F(1,26) = 16.50$, $p < 0.001$), with gains yielding more positive amplitudes compared to losses (gains: 5.15 ± 0.51 μV vs losses: 4.55 ± 0.51 μV).

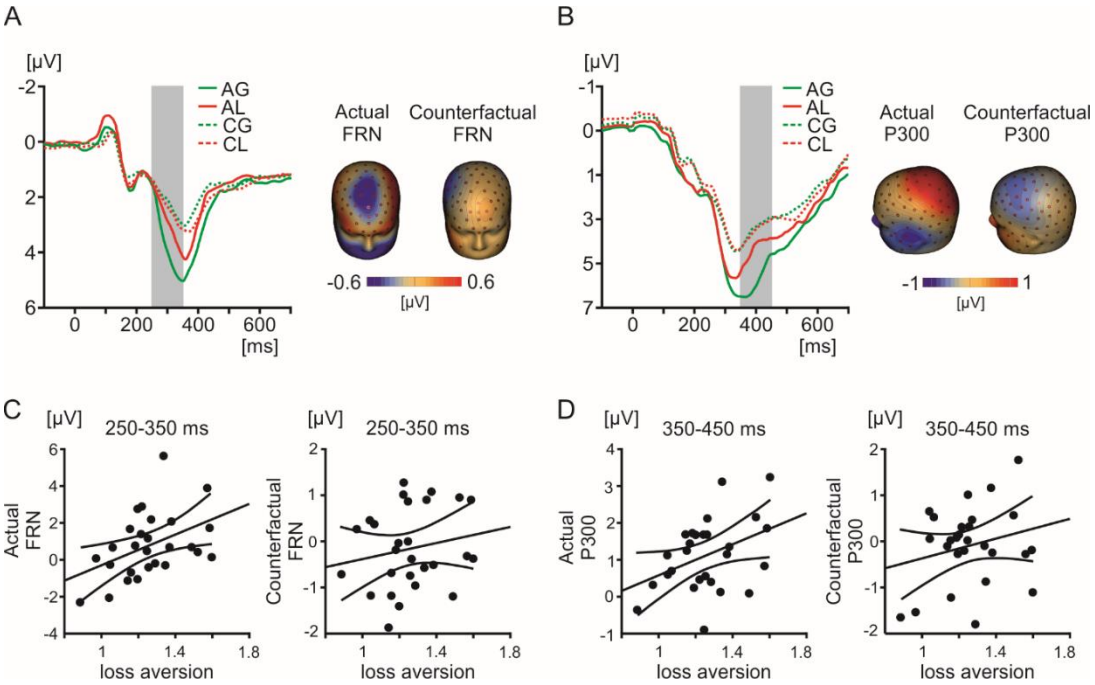

Figure 4.2. A. FRN. Left: Grand averaged EEG potentials for the four possible outcome conditions (AG = Actual Gain, AL = Actual Loss, CG = Counterfactual Gain, CL = Counterfactual Loss) pooled over the FRN electrode cluster (Fz, FCz, Cz). The grey shaded area indicates the time interval included in statistical analysis (250-350 ms). Right: Topographic maps of Actual FRN (AL minus AG) and Counterfactual FRN (CL minus CG) shown at 300 ms. B. P300. Left: Grand averaged EEG potentials for the four possible outcome conditions pooled over the P300 electrode cluster (CPz, Pz, POz). The grey shaded area indicates the time interval included in statistical analysis (350-450 ms). Right: Topographic maps of Actual P300 (AG minus AL) and Counterfactual P300 (CG minus CL) shown at 400 ms. C. Left: Scatterplot, linear regression line and 95% confidence interval lines representing the statistically significant correlation between loss aversion and Actual FRN. Right: Scatterplot, linear regression line and 95% confidence interval lines representing the lack of association between loss aversion and Counterfactual FRN. D. Left: Scatterplot, linear regression line and 95% confidence interval lines representing the statistically significant correlation between loss aversion and Actual P300. Right: Scatterplot, linear regression line and 95% confidence interval lines representing the lack of association between loss aversion and Counterfactual P300.

4.4.3 Correlations with loss aversion

Pearson's correlation analysis was carried out to investigate the relationship between loss aversion and feedback ERPs. The following difference waveforms were created: actual FRN (actual losses minus actual gains), counterfactual FRN (counterfactual losses minus counterfactual gains), actual P300 (actual gains minus actual losses), and counterfactual P300 (counterfactual gains minus counterfactual losses). Loss aversion correlated with FRN following actual outcomes ($r(27) = 0.44$, $p < 0.05$, but not with FRN following counterfactual outcomes ($p > 0.05$).

Similarly, loss aversion correlated with P300 following actual outcomes ($r(27) = 0.40$, $p < 0.05$), but not with P300 following counterfactual outcomes ($p > 0.05$). Figures 4.2C and 4.2D show the scatterplots, regression lines and 95% confidence interval lines representing the associations of loss aversion with FRN and P300, respectively.

4.5 Discussion

The present study investigated the effects of loss aversion on feedback ERPs following decision outcomes resulting from accepting or rejecting a series of gambles. The most important finding was the presence of an association between loss aversion and the strength of FRN and P300 components for actual but not counterfactual outcomes. This suggests that individual differences in loss aversion are reflected on the amplitude strength of feedback ERPs during the evaluation of those outcomes which have actual economic impact for the decision maker. Our data also extend previous research on feedback processing by demonstrating the presence of FRN and P300 potentials in a gambling task tailored to evaluate loss aversion.

4.5.1 Actual feedback

For the actual feedback condition (i.e., when participants accepted the gamble), we were able to replicate the robust FRN potential, previously observed in studies

using binary forced choice paradigms (Gehring and Willoughby, 2002; Hajcak et al., 2006; Holroyd et al., 2006; Nieuwenhuis et al., 2004b; Yeung and Sanfey, 2004). Our finding is novel in that FRN was for the first time observed in a paradigm in which participants could freely decide whether they wanted to gamble or not. In our task, participants were given complete choice freedom, and feedback was contingent upon their own decision to engage in risk-taking.

Regarding the P300 potential, our results are in accord with research highlighting its important role in outcome evaluation (Polich, 2007). Some studies have previously proposed that the P300 potential encodes reward magnitude rather than reward valence, suggesting that the brain evaluates outcomes through a double dissociation system: reward valence is encoded by FRN while magnitude is encoded by P300 (Sato et al., 2005; Yeung and Sanfey, 2004). Even though it is a limitation of the current study that potential magnitude effects were not taken into account, our results provide support to studies reporting differential processing of positive and negative outcomes at the P300 range with stronger amplitudes for gains compared to losses during economic decision making (Hajcak et al., 2005; 2007; Holroyd et al., 2006; Li et al., 2010; Wu and Zhou, 2009).

4.5.2 Counterfactual feedback

The current experiment did not find any difference in feedback ERPs to counterfactual (i.e., avoided) losses as compared to counterfactual (i.e., missed) gains. This lack of differential neural processing might seem surprising at first, especially considering the ample evidence available from fMRI studies that focused on how the brain processes missed opportunities (Camille et al., 2004; Chua et al., 2009; Coricelli et al., 2005). However, our results are in line with previous EEG research on counterfactual outcome processing by demonstrating that ERPs to foregone gains and losses share similar spatio-temporal patterns (Gu et al., 2011; Osinsky et al., 2014; Yu and Zhou, 2009). In a similar vein, Talmi et al. (2013) showed that foregone outcomes yielded similar FRN potentials, irrespective of whether these outcomes were positive (monetary reward) or negative (pain). Moreover, our results accord studies demonstrating that FRN represents an early binary evaluation of positive versus negative outcomes (Hajcak et al., 2006; Holroyd et al., 2006; Yeung and Sanfey, 2004; Yu and Zhou, 2006), and, as such, integrates only the obtained outcome valence

(Gehring and Willoughby, 2002; Kujawa et al., 2013; Yeung and Sanfey, 2004). In our task, counterfactual outcomes might have been appraised as self-irrelevant observations because they were economically neutral. This is in line with research suggesting that brain potentials when observing someone else losing money in a gambling task are weaker compared to when focusing on outcomes of one's own performance (Zhou et al., 2010), and with a general reduction of FRN amplitudes during observational feedback learning (Bellebaum et al., 2010a; Kobza et al., 2011).

It is, of course, not possible to rule out the possibility that the results might have been different if larger amounts had been used. However, by including several different amounts (ranging from £0 to £12), potential gains and losses were at least relatively large by comparing them to the smaller ones. Indeed, neuroimaging research shows that the brain adapts relatively to the range of potential amounts (Bunzeck et al., 2010; Nieuwenhuis et al., 2005a; Tobler et al., 2005). As such, based on the EEG results reported in the previous sections and although it was contrary to our initial hypothesis, participants did not consider the counterfactual loss as an economic loss relative to what they could have won. Although it cannot be ruled out that there could have been regret or disappointment involved during the processing of missed gains, this was not reflected on the EEG data.

Similarly to FRN, we did not find supporting evidence for P300 modulation by counterfactual thinking. This result is in accordance with studies reporting a lack of P300 modulation by outcome valence following counterfactual outcomes (Goyer et al., 2008; Gu et al., 2011). However, it is in contrast with some previous studies showing differential effects of counterfactual gains and losses on P300 amplitudes (Marciano et al., 2018; Osinsky et al., 2014; Yeung and Sanfey, 2004; Yu and Zhou, 2009). A possible explanation for this discrepancy rests on the difference between the tasks employed. For instance, in previous studies, participants did not have the option to completely reject gambles and, thus, the counterfactual outcome was always evaluated in association with the obtained outcome. In the present study, actual and counterfactual outcomes resulted from different decisions and, consequently, comparisons between outcomes were neither meaningful nor possible. Even though two studies (Gu et al., 2011; Marciano et al., 2018) tried to control for this comparison confound by presenting the counterfactual before the actual outcome, participants were still expecting to be presented with actual outcomes resulting from the same decision. Given that P300 has been suggested to be influenced by outcome expectation

(Bellebaum and Daum, 2008; Hajcak et al., 2007; Holroyd et al., 2004), it is possible that presence of a direct comparison of actual and counterfactual outcomes has enhanced the P300 component.

4.5.3 Loss aversion and FRN/P300

Unlike in our previous study in which loss aversion and FRN were evaluated using different tasks (Kokmotou et al., 2017), in the current study we were able to assess individual differences in loss aversion and, at the same time, relate these individual differences to FRN amplitudes recorded simultaneously. Importantly, the current study confirms the previous correlational results that showed that loss aversion measured using a behavioural task was associated with feedback potentials during a subsequent gambling task with EEG (Kokmotou et al., 2017). Specifically, in the current study, loss aversion correlated with FRN strength in fronto-central midline electrodes during 250-350 ms after feedback onset in actual but not in counterfactual outcomes.

Our results expand on two previous studies reporting associations between individual differences in loss aversion and EEG activity (Duke et al., 2018; Heeren et al., 2016). In particular, higher behavioural manifestation of loss aversion has been found to correlate with stronger resting state EEG activity in the right hemisphere (Duke et al., 2018). Additionally, loss aversion modulated a posterior slow wave potential during the decision making phase, when participants evaluated alternative prospects without expecting to learn the outcome of their decisions (Heeren et al., 2016). Furthermore, behavioural work suggests that hedonic evaluations of prospects at the time of the decision differ to those after receipt of outcomes (Kahneman et al., 1997). Neuroimaging studies further show that, during value-based decision making, the decision and outcome phase often employ different brain regions (Breiter et al., 2001; Knutson et al., 2001; Smith et al., 2009). Our results, combined with the above findings, suggest that loss aversion is associated with distinct cortical activity patterns and across different stages of the decision making process. Specifically, individual differences in loss aversion were associated with both an early medio-frontal ERP component (FRN) as well as with a later one with a more posterior activation maximum (P300).

The above association of loss aversion with FRN can be elucidated by an influential theory in the field of decision making which has proposed that risk-taking might be driven by anticipatory or experienced affective reactions towards decisions (risk-as-feelings hypothesis; Loewenstein et al., 2001). In this context, it seems possible that the relationship between loss aversion and FRN could be driven by emotional related processes as both variables have been shown to be influenced by emotions (Camerer et al., 2005; Hajcak et al., 2006; Sokol-Hessner et al., 2013; 2009). For example, loss aversion has been linked to emotions of fear or stress (Camerer et al., 2005; Hartley and Phelps, 2012). Furthermore, incidental negative emotional cues that are independent to the current decision, such as unpleasant odours (Stancak et al., 2015) or fearful faces (Schulreich et al., 2016), have the potential to increase loss aversion. Additionally, loss aversion can be decreased using emotion regulation techniques by successfully reducing the emotional impact of individual decision outcomes (Sokol-Hessner et al., 2013; 2009). Furthermore, affective ratings of pleasantness have been shown to be more negative following undesirable compared to desirable outcomes, thus, mirroring the FRN amplitude pattern (Moser and Simons, 2009; Rigoni et al., 2010). Additionally, preceding negative outcomes have been shown to induce both increased risk-taking for subsequent choices and stronger FRN amplitudes, suggesting that FRN reflects the pattern of risk-taking behaviour observed following aversive outcomes (Gehring and Willoughby, 2002; Yeung and Sanfey, 2004). Moreover, FRN has been shown to be associated with a range of emotion associated traits such as anxiety (Gu et al., 2010), reward sensitivity (De Pascalis et al., 2010; Lange et al., 2012) and impulsivity (Onoda et al., 2010). Such a potential mechanism of negative emotionality linking loss aversion and FRN is further supported by studies investigating arousal, which is an underlying emotion component (Sokol-Hessner et al., 2009; Stancak et al., 2015). For instance, monetary losses are associated with increased arousal levels compared to gains (Sokol-Hessner et al., 2009; Stancak et al., 2015) and individual differences in arousal between gains and losses correlate with loss aversion (Sokol-Hessner et al., 2009).

Importantly, such a potential emotional link, combined with the lack of difference in the electrocortical brain activity following counterfactual gains and losses, provides an explanatory context for the absence of loss aversion effects on counterfactual outcome processing. We postulate that a missed gain is not emotionally equated to an experienced loss. It has been suggested that loss aversion has an

evolutionary-based purpose, in which a monetary loss is perceived as danger or threat (Kahneman, 2011; Kenrick et al., 2009; Li et al., 2012), and, as such, it represents an emotional response to anticipated (Camerer, 2005; Tom et al., 2007) and experienced losses (Sokol-Hessner et al., 2013). In the case of counterfactual outcomes, the loss aversion mechanism has served its purpose since the feared loss has been avoided. This is consistent with an interpretation of loss aversion as a decision making bias driven by emotions (Sokol-Hessner et al., 2013), which is reduced when outcomes do not affect the individual, as, for example, when choosing for others (Andersson et al., 2014).

Similarly to FRN, loss aversion was associated with P300 strength only in the actual outcomes condition. This relationship might have been driven by two factors influencing P300 amplitude. Firstly, P300 strength differs as a function of stimulus motivational importance with stimuli that are emotionally significant for the decision maker producing higher P300 amplitudes compared to neutral or irrelevant stimuli (Duncan-Johnson and Donchin, 1977; Yeung and Sanfey, 2004). Therefore, it seems possible that, in the current study, only actual outcomes were perceived as important for participants and attended to while counterfactual ones were deliberately ignored. This is in agreement with previous research as EEG studies on counterfactual thinking have provided inconclusive results (Gu et al., 2011; Yu and Zhou, 2009; Marciano et al., 2018; Osinsky et al., 2014). Secondly, P300 has been suggested to operate as an updating process in the context of decision making (Polich, 2007). Given that only actual outcomes have the potential to influence overall payoff, it may be that participants focused on these outcomes alone to guide subsequent decisions. Taken together, loss aversion seems to correlate with both relatively early cognitive processes (FRN) and later ones (P300) following learning of decision outcomes.

Finally, investigating such a link between individual differences in loss aversion and outcome processing might enhance understanding of decision making deficits observed in various psychiatric conditions. Indeed, some psychiatric populations, such as pathological gamblers (Gelskov et al., 2016) or patients with schizophrenia (Brown et al., 2013; Currie et al., 2017; Trémeau et al., 2008) exhibit reduced loss aversion compared to healthy controls, while depressed people (Pammi et al., 2015) and people with obsessive compulsive disorder (Sip et al., 2018) show increased loss aversion. Additionally, some studies suggest that FRN is similar in schizophrenia and healthy participants, indicating normal processing of external

feedback and outcome evaluation (Horan et al., 2012; Llerena et al., 2016; Morris et al., 2011), whereas FRN is enhanced in depression (Foti and Hajcak, 2009) and diminished in obsessive compulsive disorder (Endrass et al., 2013; O'Toole et al., 2012). Specifying intact and impaired reward evaluating processes could shed light on the diminished motivation commonly seen in these disorders (Strauss et al., 2014). Further, potential absence of loss aversion might be indicative of a limited integration between emotional and cognitive systems, whereas extreme levels of loss aversion might point to a dysfunctional dominance of affective over cognitive incentives, with both cases leading to impaired value-based decision making.

To conclude, we show that feedback potentials, as indexed by FRN and P300, were correlated with individual differences in loss aversion, but only when outcomes signal a real monetary gain or loss. Given that loss aversion represents a sensitivity to losses over gains and FRN/P300 were quantified as the potential difference between outcome conditions, this association suggests a larger neural differentiation between positive and negative outcomes for the more loss averse individuals.

Chapter 5

Study 3: Sensitivity to choice freedom mediates the relationship between loss aversion and feedback-related negativity.

This experiment investigated the effects of loss aversion on the evaluation of outcomes resulting from free or obstructed decisions.

It is currently in preparation for publication in a journal to be confirmed.

5.1 Abstract

Losses tend to be overvalued compared to gains of the same amount, a phenomenon known as loss aversion. Previous studies have investigated the neural mechanisms related to loss aversion, linking it to feedback-related negativity (FRN) when participants had freedom of choice. However, real life decisions are often constrained by external factors that are outside of the decision maker's control. Whether loss aversion influences neural responses to outcomes that are externally imposed upon an individual rather than freely chosen remains to be explored. The present study analysed the effects of loss aversion on neural responses to monetary outcomes resulting from free and imposed choices using electroencephalographic (EEG) recordings. A gambling task and parametric modelling of participants' choices were employed to estimate individual differences in loss aversion. A subsequent gambling task served to evaluate neural responses to decision outcomes. Event-related potentials (ERPs) following gains and losses resulting from one's own choices (choice freedom) or from an arbitrary violation of such choices (choice violation) were analysed and correlated with loss aversion. For participants who exhibited strong neural responses to choice violation, feedback ERPs were more negative for losses resulting from free compared to forced choices, while no such effect was observed for weak responders or for gain outcomes. Crucially, loss aversion correlated with FRN only when choices were made freely and only for strong responders. Results suggest that loss aversion mediates the neural processing of outcomes exclusively when outcomes are contingent upon one's own choices and only for those participants displaying sensitivity towards having choice freedom.

5.2 Introduction

The ability to quickly and effectively evaluate obtained outcomes is an important part of the decision making process. Previous electroencephalography (EEG) studies have highlighted the importance of feedback-related negativity (FRN) in outcome evaluation (Gehring and Willoughby, 2002; Miltner et al., 1997). FRN is an event-related potential (ERP) component which differentiates between positive and negative decision outcomes (Gehring and Willoughby, 2002; Hajcak et al., 2007; Holroyd et al., 2004; Nieuwenhuis et al., 2004b; Yeung and Sanfey, 2004), and represents one of the earliest components during outcome evaluation, peaking around 200-350 ms after feedback onset (Walsh and Anderson, 2012). FRN can be elicited using simple gambling tasks in which participants select among options that can lead to monetary gains or losses (e.g., Gehring and Willoughby, 2002).

The majority of prior research investigating FRN has focused on paradigms where individuals could make unobstructed choices among offered options and, consequently, the outcomes were contingent upon their own choices (Gehring and Willoughby, 2002; Goyer et al., 2008; Hajcak et al., 2006, 2007; Holroyd et al., 2004; Kokmotou et al., 2017; Nieuwenhuis et al., 2004b). Despite this, real-world decision making is often hindered by external unforeseen circumstances that operate outside of the decision maker's control. To this end, some studies have employed paradigms that manipulate the amount of control participants have over outcomes by distinguishing between different agency levels during decision making. In particular, it has been shown that FRN is stronger following outcomes produced by choices that participants had made themselves compared to when they were passively viewing rewards that were randomly selected for them by a computer (Bismark et al., 2013; Martin and Potts, 2011; Yeung et al., 2005) or by another person deciding on their behalf (Itagaki and Katayama, 2008; Marco-Pallarés et al., 2010).

Despite these developments, previous studies still divulged to participants in advance whether they would be free to make choices or whether they would passively receive rewards (Bismark et al., 2013; Itagaki and Katayama, 2008; Marco-Pallarés et al., 2010; Martin and Potts, 2011; Yeung et al., 2005). In real world conditions, however, it is not always possible to predict when unforeseen circumstances will affect our choice, and, often, dealing with such circumstances is considered unpleasant

(Leotti et al., 2010). For instance, it has been shown that, if one initially available choice is suddenly eliminated, participants report adverse emotions (Brehm et al., 1966) and try to re-gain access to the eliminated option (Miron and Brehm, 2006). Importantly, successful adaptation to new rules and circumstances as directed by the environment is fundamental for survival, while failing to do so often negatively impacts mental health (Maier and Seligman, 1976; Shapiro et al., 1996). As such, it is important to investigate outcome evaluation in situations where choice freedom is unpredictable. To the best of our knowledge, the influence of unpredictable events that are outside of the individual's control but nevertheless influence receipt of rewards, such as being forced to choose an option other than the originally preferred one, on FRN remains to be explored.

It has also been suggested that the affective experience of having choice can be modulated by the valence of the potential outcome. For example, Leotti et al. (2014) demonstrated that when participants were faced with the possibility of gain or loss simultaneously, they reported liking having choice for cues predicting gains but were indifferent for cues predicting losses. Specifically, at the start of each trial, choice trials were differentiated from no-choice trials by cue shape (e.g., rectangle for choice trials) and the orientation of the cue (pointing upward or downward) indicated whether the trial could potentially result in monetary gain or loss. Participants learned the associations between the different cues and their respective trials prior to starting the experiment. In the choice condition, participants could freely choose between two keys, and in the no-choice condition, participants had to accept a computer-selected key. The keys were associated with different monetary amounts but participants did not know which key would yield which specific monetary amount. Instead, participants knew that, for example, in the gain trials, one key would yield a gain of £50 and the other a gain of £100. Nevertheless, having choice was associated with activity in ventral striatum for both gains and losses, a brain region commonly activated during evaluation of rewards (Delgado, 2007; O'Doherty et al., 2004). Importantly, in the case of losses, the authors observed large individual differences in the preference of having choice. They proposed that this might have been due to individual differences in sensitivity to the threat of potential loss influencing the affective experience of choice in the context of losses, although this hypothesis was not addressed directly.

In the current study, we investigated individual differences in sensitivity towards losses by focusing on loss aversion; the tendency to overestimate losses compared to gains of equivalent amount (Kahneman and Tversky, 1979). Previous studies investigating the neural underpinnings of loss aversion have linked it to activity in brain regions which are important for reward evaluation and value computation during value-based decisions, including the striatum (Canessa et al., 2017; Gelskov et al., 2015; Tom et al., 2007), the VMPFC (Tom et al., 2007), the amygdala (Canessa et al., 2013; De Martino et al., 2010; Gelskov et al., 2015; Sokol-Hessner et al., 2013) and the insula (Canessa et al., 2017; Markett et al., 2016). Importantly, loss aversion has previously been shown to be related to FRN (Kokmotou et al., 2017) and this association was modulated by situational factors (Kokmotou et al., under review). Specifically, the association between FRN and loss aversion was found for actual outcomes (i.e., outcomes resulting from gambles chosen by the individual), but not for counterfactual outcomes (i.e., outcomes that did not have any economic impact for the individual) resulting from unchosen gambles. As economically neutral outcomes were considered those that did not lead to any positive or negative monetary outcome. Of course, it cannot be ruled out that these outcomes were psychologically different. Although a counterfactual gain (i.e., gain that the participant missed but could have won if they decided differently) could potentially signify loss relative to what could have been won, similar to fMRI studies (Camille et al., 2004; Coricelli et al., 2005), this was not the case in the above study, a finding which is further in agreement with other EEG studies on counterfactual outcomes (Marciano et al., 2018; Yeung and Sanfey, 2004; Yu and Zhou, 2009). Crucially, counterfactual outcomes in the above study were not motivationally relevant for individuals since they were economically neutral. This suggests that, when participants were free to choose, loss aversion was not associated with the evaluation of outcomes that did not impact them. Therefore, the relationship between loss aversion and unchosen outcomes that do have an economic impact for participants remains to be explored.

The aim of the present study was to investigate the influence of individual differences in loss aversion on FRN following monetary reward or penalty resulting either from participants' free choice or from an arbitrary obstruction of choice. A gambling task and parametric fitting of choices were used to evaluate loss aversion (Kokmotou et al., 2017; Sokol-Hessner et al., 2013; 2009; Stancak et al., 2015) while a second gambling task was used to measure FRN (Gehring and Willoughby, 2002)

under two choice conditions. In the choice freedom condition, participants chose between two risky gambles, each offering 50% chance of winning or losing and received the outcome (gain or loss) from their chosen gamble. In the choice violation condition, participants received the outcome from the unselected gamble. FRN was evaluated separately for each choice condition and correlated with loss aversion values. Given that previous studies reported large individual differences in the preference of having choice (Leotti et al., 2014), it was hypothesised that individual differences in sensitivity to having choice freedom, as indicated by strength of neural activity in each choice condition, would mediate the relationship between loss aversion and FRN.

5.3 Methods

5.3.1 Participants

A total of twenty-seven healthy participants (14 females) completed the study. After the exclusion of three participants who displayed extremely high values of loss aversion (> 3 SDs from the mean), similarly to previous studies (Sokol-Hessner et al., 2009), the final sample consisted of 24 participants (13 females), 4 left-handed, aged 22.57 ± 2.31 years (mean ± SD). The study was approved by the Research Ethics Committee of the University of Liverpool. All participants gave written informed consent in accordance with the Declaration of Helsinki.

5.3.2 Procedure

Participants first completed a monetary gambling task which was used to elicit individual loss aversion values. Risk aversion and choice sensitivity were also evaluated but, similar to Chapter 4, they were not associated with brain data. Participants were endowed with £20 to use for gambling and were informed that they could increase or decrease this amount depending on their choices. Figure 5.1 shows the trial structure. Participants were required to choose between a gamble and a certain outcome. The gamble offered 50% chance of winning or losing variable amounts of

money. The alternative certain outcome was either zero or an amount smaller than the potential gain from the corresponding gamble in a particular trial. If participants accepted the gamble, feedback was given about whether the trial was won or lost, whereas, if they rejected the gamble, they proceeded to the next trial. Feedback was not given for rejected gambles because in this case participants have selected the sure option (i.e., the option associated with 100% probability to receive the stated outcome). As such, participants could know what they have received without needing to be given any feedback. That was the case both when they received £0 and when they received other amounts, irrespective of whether these amounts were small or large. For instance, if a participant had to select between a gamble and a sure gain of £2, they knew that if they selected the gain they would receive it with 100% probability. Therefore, as soon as they selected it, they knew they would receive it. As such, the reason for which feedback was not given in this case was because it was not needed. Participants made a total of 200 such choices that allowed for estimation of individuals' decision making style by calculating loss aversion based on prospect theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992). The exact gamble amounts, value and logit functions and numerical approximation method used were reported in detail in previous studies (Kokmotou et al., 2017; Stancak et al., 2015). Participants received the accumulated amount from a randomly selected 10% of the trials in addition to the initial endowment as reimbursement for participating in the experiment.

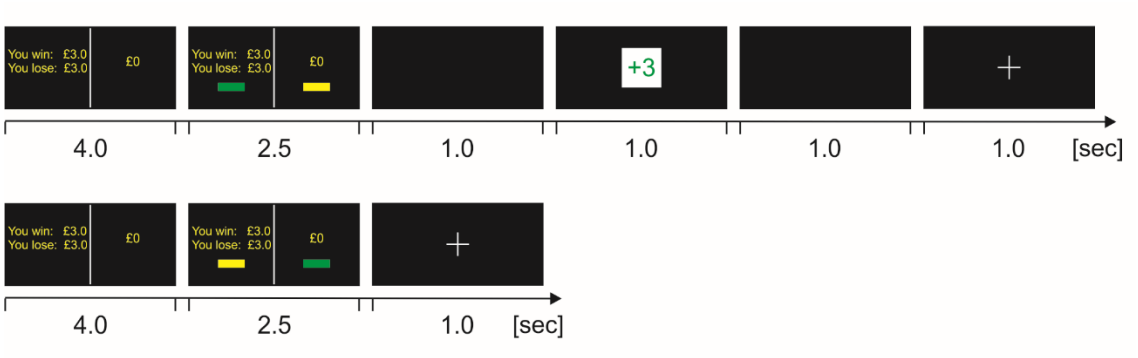

Figure 5.1. Trial structure of the loss aversion task. Each trial began with the presentation of two prospects, which stayed on the screen for 4 s. Half of the screen presented a gamble option offering 50% chance of winning or losing the displayed amount of money (e.g., 'You win £3.0, You lose £3.0'). The other half of the screen presented a sure outcome (e.g., £0). Subsequently, two yellow rectangles appeared under each prospect and participants had 2.5 s to select the rectangle corresponding to the option they preferred by pressing the left or right mouse button. Their chosen rectangle turned green to highlight their choice and was followed by a 1 s black screen. Next, if participants accepted the gamble (top panel), feedback was given about the gamble outcome. This feedback constituted of the monetary amount in green colour with a '+' sign or red colour with a '-' sign for gains and losses, respectively, and stayed on the screen for 1 s. One more 1 s black screen appeared before the start of the next trial. If participants chose the sure option (bottom panel), they proceeded to the next trial. If participants rejected the gamble, there was no reason to give feedback because they already knew what the outcome was since the sure option was associated with 100% probability to receive the outcome. In the example above, participants knew that they received £0 since they chose this option, therefore, there was no reason to receive feedback. This was the case with all experiments that used this task. Giving them feedback would not have any advantage either in terms of behavioural or EEG data.

5.3.3 Choice violation/FRN task

Following the loss aversion task, participants were connected to the EEG system and completed a second gambling task during which they could win or lose money either as a result of their own choice or irrespective of their choice. The task was adapted from previous FRN studies (Gehring and Willoughby, 2002). Figure 5.2 shows the trial structure. Each trial began with the presentation of two white cards positioned next to each other. After 1 s, the numbers 25 and 5 appeared in each of the cards, indicating amount of money in pence to be potentially won or lost on that trial. The two cards never contained the same number simultaneously. Participants were required to choose, at their own pace, one of the cards but were informed that their choice could be arbitrarily swapped for the unchosen card. After participants had chosen their preferred card, a yellow frame appeared around it for 1 s. A black screen was then presented for 1 s serving as a resting interval. Next, participants received feedback (henceforth 'choice feedback') about whether their original choice was retained ('unchanged') or swapped for the opposite card ('changed'). If their original choice was retained, participants were presented again with their originally chosen card surrounded by the yellow frame, whereas, if it was changed, participants saw the yellow frame surrounding the unchosen card. The choice feedback interval lasted for 2.5 s. It was emphasised to the participants that they would receive the outcome (gain or loss) of the final chosen gamble (i.e., the one surrounded by the yellow rectangle after the choice feedback) irrespective of whether that was their original choice or not. Thus, the choice feedback was economically neutral for participants because both the chosen and the alternative card could lead to monetary gain or loss. Unbeknownst to participants, the chosen card was swapped for the opposite in half of the trials. After the choice feedback, another black screen was shown for 1 s. Finally, participants received feedback about the outcome of the gamble (henceforth 'outcome feedback'). The chosen and the unchosen cards were displayed again with the sign of '+' or '-' in front of each number, indicating amount won or lost, respectively. Additionally, the yellow frame changed to green colour to represent gains and red to indicate losses. The outcome on any trial was predetermined by the computer so that gains and losses occurred with equal probability (i.e., 50%). The combination of choice and outcome feedback produced four possible outcomes: 1) the original choice was retained and

participant won (‘unchanged/gain’), 2) the original choice was retained and participant lost (‘unchanged/loss’), 3) the original choice was swapped for the unchosen card and participant won (‘changed/gain’), and 4) the original choice was swapped for the unchosen card and participant lost (‘changed/loss’).

The task consisted of 384 trials, split into 12 blocks of 32 trials with the duration of each block being approximately 6 min. At the end of each block, participants received feedback about the amount of money earned in that block as well as the accumulated amount gained from the beginning of the task. Participants kept the total difference between their gains and losses from all trials of that task.

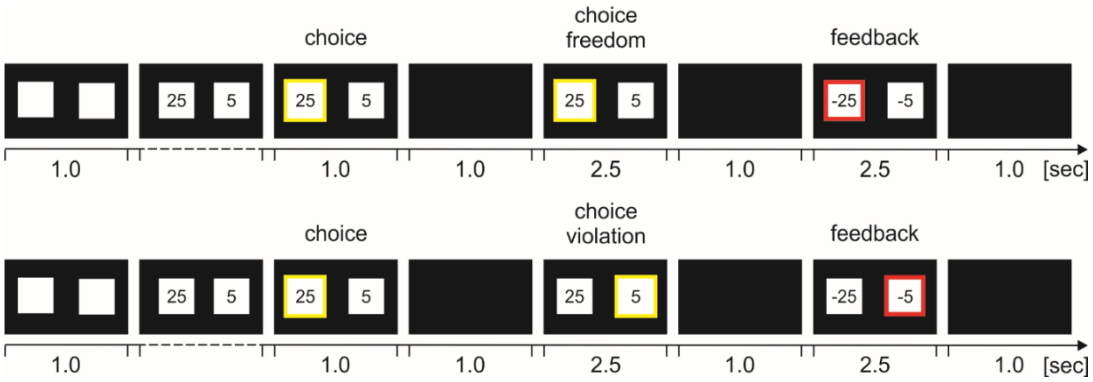

Figure 5.2. Trial structure of the FRN task. Each trial began with the presentation of two white rectangles positioned next to each other (one on the left and one on the right side of the screen) on a black background. After 1 s, the numbers 25 and 5 were presented in either one of the rectangles, indicating amount of money (in pence). Participants had to choose between these two options by pressing the left or right mouse button, and their chosen option was highlighted for 1 s with a yellow rectangle. This was followed by a 1 s black screen. Afterwards, participants received choice feedback. In the choice freedom condition, they saw again the choice screen with their selected rectangle being surrounded by a yellow rectangle (top panel). In the choice violation condition, they saw the yellow rectangle surrounding the opposite card (bottom panel). In both choice conditions, the choice feedback was followed by a 1 s black screen, and after this, outcome feedback was presented whereby the chosen and the unchosen cards were displayed again with the sign of ‘+’ or ‘-’ in front of each number, indicating amount won or lost respectively. Additionally, the yellow frame changed to green colour to represent gains and red to indicate losses. This outcome feedback stayed on the screen for 2.5 s and was followed by a 1 s black screen before the beginning of the next trial.

5.3.4 EEG Recordings

During the choice violation/FRN task, participants were connected to a 129-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. The sensor net was aligned with respect to three anatomical landmarks; two preauricular points and the nasion. Electrode-to-skin impedances were kept below 50 kΩ, as recommended for this system (Ferree et al., 2001; Picton et al., 2000). The recording band-pass filter was 0.01−200 Hz, and the sampling rate was 1000 Hz. The electrode Cz served as the reference.

EEG data were pre-processed using BESA v. 6.1 program (MEGIS GmbH, Germany). EEG signals were spatially transformed to reference-free data using the common average reference method (Lehmann, 1987). Eye blinks and, when necessary, electrocardiographic artifacts were removed using principal component analysis (Berg and Scherg, 1994), while data were also visually inspected for the presence of any electrode artifacts due to muscle movement, and epochs contaminated with artifacts were excluded. Data were filtered from 0.5−35 Hz.

5.3.5 Statistical analysis

For statistical analysis, EEG data were exported to Matlab v. R2017a. Grand averaged ERPs from the two choice feedback conditions were compared statistically using a series of paired samples t-tests for each time sample from 300 to 600 ms following the presentation of choice feedback. Grand averaged ERPs from the four outcome feedback conditions were analysed with a two-way repeated measures ANOVA in the epoch from 200 to 300 ms following outcome feedback onset with choice feedback (unchanged vs changed) and outcome feedback (gain vs loss) as factors. Statistical significance was evaluated using permutation analysis (Maris and Oostenveld, 2007) with 5000 permutations in EEGLAB v.12 (Delorme and Makeig, 2004). Averaged data from time intervals showing statistically significant effects were exported to SPSS Statistics software v. 22.0 (IBM Corp, 2013) for further analysis. Pearson's correlation analysis was used to investigate linear associations between loss aversion and ERPs. A 95% confidence interval was employed.

5.3.6 ERP analysis

The ERP analysis included two steps. First, ERPs time-locked to the presentation of choice feedback (unchanged/changed) were computed by averaging respective epochs during the interval from 100 ms before to 1000 ms after choice feedback. Epochs were baseline corrected using a time window of -100 ms to 0 ms relative to the onset of the choice feedback. A difference waveform was computed by subtracting ERPs in response to changed choice from ERPs in response to unchanged choice feedback (unchanged-minus-changed difference waveform). The mean number of accepted trials was 180.66 ± 1.79 and 182.62 ± 1.57 (mean ± SEM) for changed and unchanged choice condition, respectively.

Second, ERPs time-locked to outcome feedback (gain/loss) were computed for each of the four possible outcome conditions (unchanged/gain, unchanged/loss, changed/gain, changed/loss) by averaging respective epochs from 100 ms before to 1000 ms after outcome feedback. Epochs were baseline corrected using a time window of -100 ms to 0 ms relative to the onset of the outcome feedback. FRN was quantified as the potential difference after subtracting loss from gain ERPs for each of the choice feedback conditions. This resulted in 'unchanged FRN' (unchanged/gain-minus-unchanged/loss difference waveform) and 'changed FRN' (changed/gain-minus-changed/loss difference waveform). The mean number of accepted trials per condition was as follows: changed/gain: 92.04 ± 1.74, changed/loss: 90.85 ± 1.35, unchanged/gain: 92.12 ± 1.21, unchanged/loss: 91.70 ± 1.49.

5.4 Results

5.4.1 ERPs in response to choice feedback

To explore brain responses following choice feedback, ERPs for trials where participants' choice was changed to the opposite option (changed) were compared against trials where their original choice was retained (unchanged). Figure 5.3A shows grand averaged ERPs in response to choice feedback, the difference waveform between these two conditions (unchanged-minus-changed) and the corresponding topographic maps. The difference potential peaked approximately 380 ms after

presentation of choice feedback and showed a positive maximum at vertex electrodes protruding towards posterior electrodes. The selection of electrodes to be used for statistical analysis was based on the objective of choosing a cluster of electrodes where differences between conditions of interest were the strongest (Yu and Zhou, 2010). The resulting cluster consisted of six electrodes including Cz and five adjacent to it extending posteriorly (EGI electrodes 31, 54, 79, 80 and 55).

A paired samples t-test was carried out at each time point from 300 to 600 ms after choice feedback to investigate differences between ERPs in response to 'unchanged' and 'changed' choice conditions. Statistically significant differences were seen between 340-540 ms after choice feedback (shaded area in Figure 5.3A). A paired samples t-test on averaged data from this time window showed that 'unchanged' choices yielded significantly stronger amplitudes compared to 'changed' choices (unchanged: 1.74 ± 0.24 μV, changed: 1.12 ± 0.23 μV; $t(22) = 5.62$, $p < 0.001$). Further analyses showed that the difference between changed and unchanged ERPs was invariant to the selection of particular electrodes in the potential maximum at the vertex (Pz: $t(23) = 4.61$, $p < 0.001$, unchanged: 1.82 ± 0.30 μV, changed: 1.17 ± 0.26 μV; CPz: $t(23) = 3.82$, $p < 0.001$, unchanged: 1.79± 0.23 μV, changed: 1.21 ± 0.23 μV; Cz: $t(23) = 6.16$, $p < 0.001$, unchanged: 1.68 ± 0.24 μV, changed: 1.06 ± 0.21 μV). To further ensure that the findings were independent of the selected time window, a permutation analysis was conducted for each electrode and yielded very similar results (Pz 359-562 ms: $t(23) = 4.89$, $p < 0.001$, unchanged: 1.68 ± 0.29, changed: 1.03 ± 0.25; CPz 351-507 ms: $t(23)=3.61$, $p < 0.001$, unchanged: 1.90 ± 0.25, changed: 1.27 ± 0.24; Cz 334-529 ms: $t(23) = 6.05$, $p < 0.001$, unchanged: 1.73 ± 0.29, changed: 1.09 ± 0.22).

5.4.2 ERPs in response to outcome feedback

To evaluate effects of choice feedback on ERP amplitudes during the outcome receipt phase, ERPs to gain and loss outcomes resulting from both unchanged and changed choices were analysed. Figure 5.3B shows the grand averaged waveforms of the four outcome conditions, their corresponding topographic maps and the topographic maps of the two FRN difference waveforms (changed and unchanged FRN). The FRN waveforms showed a peak at approximately 230 ms and both

demonstrated a positive maximum over the vertex. A central midline electrode cluster including Cz and FCz as well as the two electrodes positioned immediately between them (EGI electrodes 6 and 7) was selected for statistical analysis.

To investigate effects of choice (unchanged vs changed) and outcome feedback (gain vs loss) on ERPs, a two-way repeated measures ANOVA was carried out at each time point over a latency interval of 200 to 300 ms after outcome feedback onset. The ANOVA yielded a statistically significant main effect of outcome (gain vs loss) during 220-290 ms after feedback presentation (shaded area in Figure 5.3B). Paired samples t-tests on averaged data from this time window showed that losses yielded significantly more negative amplitudes compared to gains (losses: 0.69 ± 1.62 μV, gains: 1.17 ± 1.65 μV; $t(22) = 4.74$, $p < 0.001$), revealing a typical FRN effect. Contrary to our hypothesis, there was neither a significant main effect of choice feedback nor an interaction between choice and outcome feedback on ERPs (*ps* > 0.05), suggesting that brain responses after learning the gamble outcome were only modulated by outcome valence irrespective of whether this outcome stemmed from participants' own choice or not.

5.4.3 Associations of loss aversion with choice and outcome ERPs

To investigate associations of loss aversion with choice and outcome feedback ERPs, three Pearson's correlation analyses were carried out between loss aversion and each of the three difference potential waveforms (unchanged-minus-changed, changed FRN and unchanged FRN) in the time intervals of the statistically significant differences between conditions (340-540 ms for choice feedback and 220-290 ms for FRN). There was no statistically significant correlation between loss aversion and either difference waveform (*ps* > 0.05).

5.4.4 Effects of individual differences in response to choice violation on FRN

To analyse individual differences in the appraisal of choice violation feedback, a median split of the amplitudes of the unchanged-minus-changed difference waveform was used to divide the sample into those participants who responded weakly to the change of their choice and those who responded strongly. Figure 5.3C shows

grand averaged waveforms of the outcome feedback conditions for weak and strong responders to choice change.

To investigate differences in outcome feedback ERPs for weak and strong responders to the choice violation feedback, a 2×2×2 repeated measures ANOVA was performed on 220-290 ms after outcome feedback with choice (unchanged vs changed), outcome (gain vs loss) and choice change response level (weak vs strong) as factors. The ANOVA yielded a significant main effect of outcome type (gain vs loss) on ERPs ($F(1,22) = 29.05$, $p < 0.001$), echoing the first analysis. A paired samples t-test on averaged data indicated that losses yielded significantly more negative amplitudes compared to gains (losses: 1.12 ± 0.42 μV, gains: 1.75 ± 0.45 μV; $t(23) = 5.51$, $p < 0.001$). Neither the main effect of choice violation nor the main effect of response level reached significance ($p > 0.05$).

The ANOVA yielded a statistically significant interaction between choice change and outcome feedback ($F(1,22) = 9.001$, $p < 0.05$). Post-hoc pairwise comparisons revealed that this interaction was driven by ERPs in response to losses, with ERPs to 'changed/loss' feedback being significantly stronger than ERPs to 'unchanged/loss' feedback (changed/loss: 1.29 ± 0.43 μV, unchanged/loss: 0.95 ± 0.41 μV; $t(23) = 2.85$, $p < 0.05$). In contrast, ERPs in response to gains were similar for both levels of choice feedback ($ps > 0.05$). Neither the interaction between response level and choice feedback nor the one between response level and outcome type were significant ($ps > 0.05$).

Most importantly, the three-way interaction between choice feedback, outcome type and response level was statistically significant ($F(1,22) = 5.29$, $p < 0.05$). Figure 5.3D depicts mean ERP amplitudes of the four outcome conditions for weak and strong responders. Post-hoc t-tests revealed that this interaction was driven by ERPs in response to losses, with 'changed/loss' being significantly stronger than 'unchanged/loss' for the strong response condition (changed/loss: 1.58 ± 0.51 μV, unchanged/loss: 1.06 ± 0.55 μV; $t(11) = 2.78$, $p < 0.05$). In contrast, gains were similar across both choice feedback and response levels. Results suggest that choice violation affected only those participants who responded strongly to the switching of their original choice for an arbitrarily imposed choice and only when choices led to losses.

5.4.5 Correlations with loss aversion

A Pearson's correlation analysis was carried out to investigate associations between loss aversion and FRN in those participants who responded strongly versus weakly to the choice change. A statistically significant correlation was found between loss aversion and 'unchanged FRN' for strong responders ($r(12) = 0.68$, $p < 0.05$). In contrast, no significant associations were found between loss aversion and either of the remaining FRN waveforms (strong changed FRN: $r(12) = 0.19$, weak unchanged FRN: $r(12) = 0.28$, weak changed FRN: $r(12) = 0.25$, $ps > 0.05$). Figure 5.3E shows the scatterplots and linear regression lines of the above correlations. Results suggest that loss aversion was associated with FRN only when participants responded strongly to choice change and only when outcomes originated from their own choices.

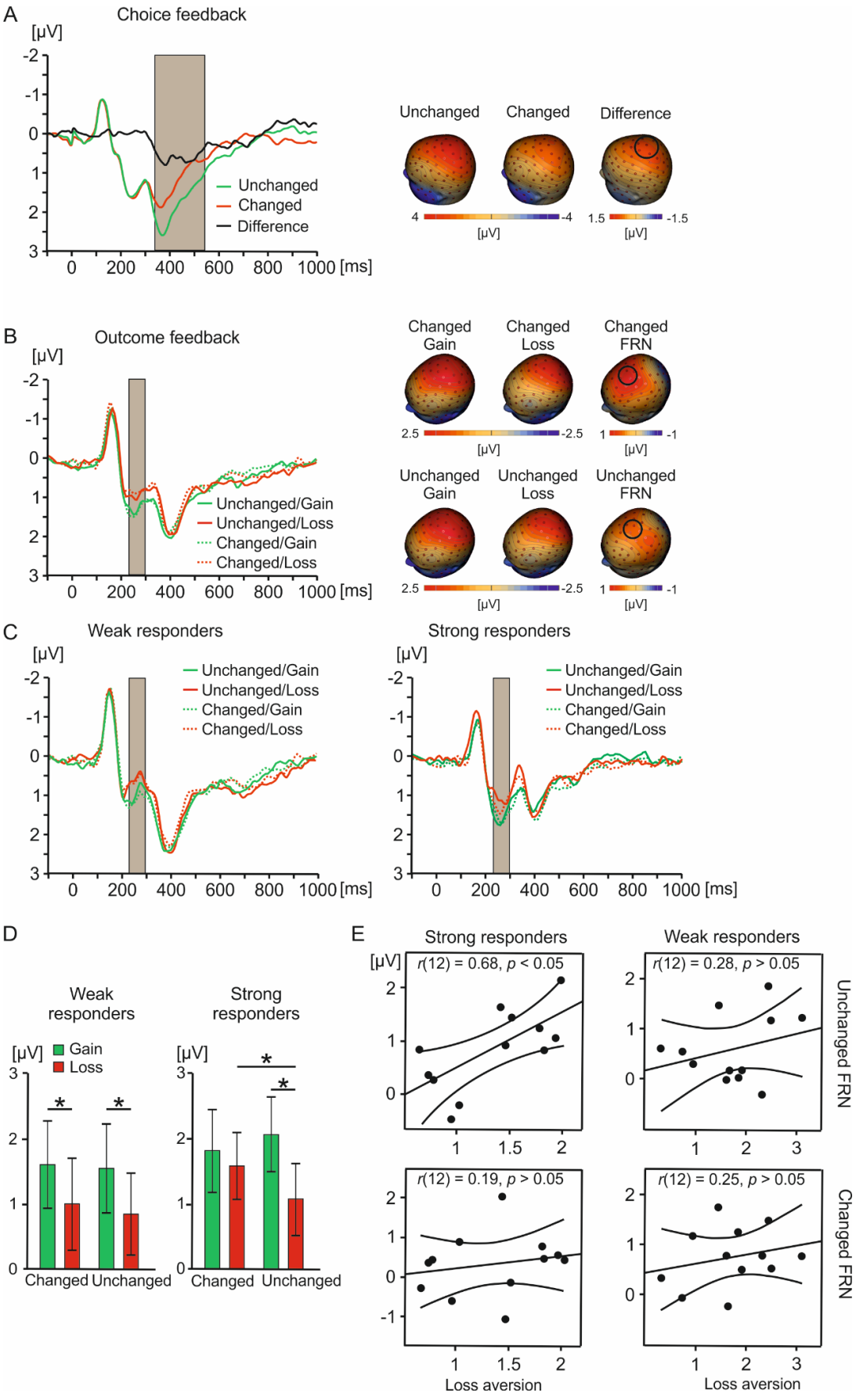
A
Choice feedback
[μV]
-2
-1
0
1
2
3
0
200
400
600
800
1000 [ms]
Unchanged
Changed
Difference
Unchanged
Changed
Difference
4
-4
[μV]
1.5
-1.5
[μV]
B
Outcome feedback
[μV]
Unchanged/Gain
Unchanged/Loss
Changed/Gain
Changed/Loss
Changed Gain
Changed Loss
Changed FRN
2.5
-2.5
[μV]
1
-1
[μV]
Unchanged Gain
Unchanged Loss
Unchanged FRN
C
Weak responders
Strong responders
D
Weak responders
Strong responders
[μV]
Gain
Loss
Changed
Unchanged
E
Strong responders
Weak responders
r(12) = 0.68, p < 0.05
r(12) = 0.28, p > 0.05
r(12) = 0.19, p > 0.05
r(12) = 0.25, p > 0.05
Unchanged FRN
Changed FRN
Loss aversion
Loss aversion

Figure 5.3. A. Grand averaged EEG potentials for the two choice feedback conditions and their difference waveform (left). The shaded area corresponds to the time interval of the statistically significant differences between 'unchanged' and 'changed' feedback (340-540 ms). Topographic maps of choice feedback and the difference potential shown at the peak (380 ms) of the difference waveform (right). The black circle indicates the electrode cluster entered into statistical analysis. B. Grand averaged EEG potentials for the four outcome feedback conditions (left). The shaded area corresponds to the time interval of the statistically significant main effect of outcome type (220-290 ms). Topographic maps of each outcome feedback condition and the difference potentials (right). The black circles indicate the electrode cluster entered into statistical analysis. C. Grand averaged EEG potentials for the four outcome feedback conditions split into weak and strong responders to choice feedback. The shaded areas correspond to the time interval of the statistically significant main effect of outcome type (220-290 ms). D. Bar graph illustrating the mean EEG amplitudes per condition. Asterisks indicate statistical significance. E. Scatterplots and linear regression lines representing the correlations between loss aversion and FRN. Confidence intervals are set at 95%.

5.5 Discussion

The present study identified two parameters as essential in order for loss aversion to be associated with the neural evaluation of decision outcomes: participants must display sensitivity to choice freedom and decision outcomes must be a product of the participant's own decisions. A separation of the sample into participants who responded weakly versus strongly to the lack of choice freedom revealed that responses to losses rather than gains were more pronounced for strong responders. Moreover, we showed that the classic FRN effect was present in both choice freedom and choice violation conditions, which aligns with studies suggesting that this component represents a coarse binary dissociation between positive and negative outcomes (Yeung and Sanfey, 2004).

5.5.3 ERPs following choice feedback

Following selection of their preferred option, participants received feedback regarding whether this option would actually occur. An ERP component manifesting approximately 300-500 ms after receipt of choice feedback was more pronounced in the choice freedom compared to the choice violation condition. Based on the latency

of its peak, approximately at 380 ms after choice feedback, as well as its centro-parietal topography, this component is thought to represent the P300 potential component (Polich, 2007, 2012).

Previous research has indicated that the P300 plays important role in decision making and stimulus evaluation, encoding attentional and motivational mechanisms (Donchin et al., 1978; Polich, 2007). Moreover, some researchers have shown that the P300 is sensitive to the degree of personal responsibility experienced, with P300 amplitudes being stronger in high compared to low responsibility conditions (Li et al., 2011; 2010; Zhou et al., 2010). In the present study, the choice freedom condition may have produced an element of personal responsibility for participants due to the contingency of the decision outcome with their own actions. Likewise, the ability to choose freely produces an increased sense of personal control (Rotter, 1966), while the mere action of having choice leads to enhanced intrinsic motivation and perceived competence (Leotti and Delgado, 2011; 2010). Importantly, the P300 has previously been shown to be stronger for stimuli that are task-relevant and motivationally significant (Polich, 2007). In a similar vein, the choice freedom condition is likely to have been more motivationally significant for participants compared to the choice violation condition due to perceived increased control over decision outcomes, thus, leading to increased P300 amplitudes.

5.5.2 ERPs following outcome feedback

When focusing on ERPs following outcome feedback, irrespective of individual differences in sensitivity towards choice freedom, the classic FRN effect was observed, with monetary losses yielding more negative amplitudes compared to gains (Gehring and Willoughby, 2002; Miltner et al., 1997). Importantly, the FRN was observed in both choice freedom and choice violation conditions. This finding is consistent with previous FRN studies in the sense that the brain segregates positive and negative outcomes irrespectively of the context in which the outcome was produced (Hajcak et al., 2006).

It is possible that the FRN component in the choice violation condition in the current study is comparable to the observational FRN previously reported in tasks where participants passively viewed the delivery of rewards and made no overt choices

(Bismark et al., 2013; Itagaki and Katayama, 2008; Marco-Pallarés et al., 2010; Martin and Potts, 2011; Yeung et al., 2005). However, an important difference is that observational FRN studies report stronger FRN amplitudes in the active compared to the passive choice condition (Bismark et al., 2013; Itagaki and Katayama, 2008; Marco-Pallarés et al., 2010; Martin and Potts, 2011; Yeung et al., 2005), whereas the current study observed similar amplitudes in both choice conditions. Therefore, if FRN in the current study was simply observational in nature, a smaller FRN amplitude would have been observed in the choice violation condition. This discrepancy, taken together with the choice condition differentiation by the P300 component, is likely an indicator that the manipulation of choice freedom was successful. Participants did not appraise outcomes in the choice violation condition as passive rewards, but rather, outcomes appear to be evaluated in a different way, which is perhaps sensitive to individual differences related to the frustration associated with the disruption of choice (Leotti et al., 2010).

5.5.3 Effects of individual differences in sensitivity to choice violation on FRN

When individual differences in sensitivity to having choice freedom were considered, choice condition modulated the evaluation of decision outcomes, but only for those participants who were sensitive to retaining their choice freedom. Sensitivity to choice freedom was defined as the degree to which participants differentiated between choice freedom and choice violation conditions at the neural level, based on the difference in P300 amplitudes between the two conditions. The rationale for this comes from behavioural studies reporting individual differences in the way people experience having choice, with some being more sensitive to choice freedom and others more indifferent (Leotti and Delgado, 2014; Patall et al., 2008; Ryan and Deci, 2006). To the best of our knowledge, this is the first study to investigate such differences at the neural level and to analyse their influence on loss aversion and feedback ERPs.

Importantly, in our study, the modulation of outcome evaluation by choice condition occurred only for losses, which can be seen in Figure 5.3D. In contrast, both chosen and unchosen gains yielded similar amplitudes, suggesting that positive outcomes were keenly received irrespective of their source. The differences observed

for losses might be indicative of feelings of unfairness or of a general tendency to attribute failure to external factors (Brewin and Shapiro, 1984; Gregory, 1978; Rotter, 1966). Along those lines, Leotti et al (2014) demonstrated the importance of outcome valence as a moderating factor in both behavioural measures of preference for having a choice and neural activation at the time of choice. Specifically, when both loss and gain outcomes were equally likely to occur, losses were associated with decreased preference for having choice. However, when participants were faced only with potential losses and had to try to avoid them, choice preference shifted towards levels similar to those for gains. Additionally, striatum activity associated with preference for having choice was modulated by outcome valence. In particular, during choice cues, which cues were different geometrical shapes associated with either a free-trial where participants had choice or a forced-trial where participants did not have a choice and just received an option randomly selected by the computer, the striatum was activated only for potential gains in the context of both gains and losses, and was also activated when choices could only lead to losses but not to gains. Furthermore, previous fMRI studies have demonstrated that when rewards are actively chosen by individuals, compared to passively delivered rewards, receipt of those rewards is associated with stronger activation of the striatum (Bjork and Hommer, 2007; O'Doherty et al., 2004; Tricomi et al., 2004), a region linked to emotional and reward-related processing (Delgado, 2007). In addition, it has been shown that voluntary, rather than involuntary, risk taking is associated with activation in a range of brain regions relevant for reward-processing (Rao et al., 2008). Our finding that both agency and outcome valence contribute to the way in which decision outcomes are appraised on the cortical level aligns with the above fMRI studies.

Regarding participants that were relatively indifferent to having choice in the current study, the lack of FRN modulation by choice condition suggests that they did not appear to be sensitive to how monetary outcomes were obtained, in the case of both rewards and penalties. It could be argued that, in the current task, this was rational behaviour given that outcomes were randomly selected by the computer in both choice conditions. In terms of cognitive load theory (Paas et al., 2003; Sweller, 1988, 1994, 2011) and economic models of rational choice, the choice condition feedback could be ignored altogether as it has no real influence over outcomes. In this sense, it may be that by not emotionally engaging in feedback that was irrelevant for their goals, those participants behaved more rationally.

5.5.4 Loss aversion and FRN

In the current study, loss aversion was correlated with FRN amplitude following outcomes resulting from unobstructed choices for participants who showed sensitivity to having choice freedom during 220-290 ms after feedback. This finding replicates our previous study, which, using a similar paradigm and experimental procedures, demonstrated that loss aversion was associated with FRN during 233-263 ms after feedback onset (Kokmotou et al., 2017). In addition, it provides support to other studies, which, using experimental paradigms more suited to measure loss aversion, revealed similar associations between loss aversion and feedback ERPs (Kokmotou et al., under review).

Another study investigated the influence of loss aversion on electrocortical potentials at the time of the decision. In particular, Heeren et al. (2016) showed that loss aversion mediated a posterior positive slow potential when participants were reflecting upon gambles with small gain/loss ratios which were indicative of high decision conflict. The authors report that this association was modulated by individual differences in trait loss aversion. Specifically, for individuals high in loss aversion, this posterior positive component was decreased both for high and low conflict decisions. The authors suggest that this indicates a relative negativity associated with conflict detection depending on trait loss aversion. Taken together with the fact that loss aversion has been theorised to represent an emotional mechanism that acts to avoid the negative emotionality associated with potential losses (Sokol-Hessner et al., 2013; 2009), we postulate that loss aversion and FRN represent behavioural and neural manifestations of the same phenomenon: differential sensitivity to the valence of reward. Loss aversion is an emotional discomfort at the possibility of an upcoming threat, whereas FRN is the affective evaluation of that threat after an outcome has been obtained.

Importantly, the lack of association between loss aversion and FRN under specific conditions has implications for outcome evaluation theories and for literature on the neural underpinnings of loss aversion by determining exceptions in its manifestation. Specifically, in the current study, loss aversion lacked relevance during outcome evaluation under three conditions; when individual differences in choice sensitivity were unaccounted for, when participants were indifferent towards having

choice freedom, and when outcomes were not contingent upon the participant's choice. Firstly, when the whole sample was included in the analysis, loss aversion was not associated with FRN, in contrast to our previous study (Kokmotou et al., 2017). However, these contradicting findings can be reconciled by studies on observational learning (Bellebaum et al., 2010a). Several studies have shown that FRN following outcomes resulting from free choices is stronger compared to mere observation of such outcomes in which the individual has no agency (Bellebaum et al., 2010a; Coricelli et al., 2005). In this sense, we postulate that by including the choice violation manipulation, we induced a mixture of self and observational FRN which is different compared to the FRN we previously obtained from one single choice condition. This resembles our findings for when outcomes were considered self-irrelevant because they were counterfactual (Kokmotou et al., under review) and when outcomes influenced others but not the participant (Kokmotou et al., in preparation). Secondly, regarding the lack of an association between loss aversion and FRN for participants responding weakly to the change of their choices, we cannot rule out the possibility that this part of the sample may not have fully engaged in the task, may not have believed in the rules described, or may have become frustrated due to the lack of control and, consequently, became inattentive (Leotti et al., 2010). Finally, regarding the changed FRN for strong responders, it may be that they did not perceive the outcomes from changed choices as their own. Support for this interpretation comes from one study which showed that FRN was sensitive to subjective expectations about gambling outcomes (Moser and Simons, 2009). Participants were asked to report whether they thought that their selected gamble would win or lose at two time points; immediately after making a choice and just before learning the outcome. Results showed that in the condition where participants stuck to their initial guess, subjective reports of outcome expectations and ERPs associated with those outcomes were both stronger compared to when participants changed their original guess. Therefore, this finding could be indicative of decreased ownership at the time of the decision (Moser and Simons, 2009) and decreased control over action outcomes (Leotti et al., 2010), as individuals may assume different levels of responsibility when they have different levels of control over outcomes (Coricelli et al., 2005; Walton et al., 2004).

The above findings add to previous studies suggesting that, like most phenomena, loss aversion is context dependent (Novemsky and Kahneman, 2005). For instance, studies have shown that loss aversion is absent for small amounts of money

(Harinck et al., 2007) and reduced when decisions are considered part of a broader portfolio of choices (Sokol-Hessner et al., 2013; 2009), or when decisions influence others (Andersson et al., 2014). In addition, one fMRI study showed that successful reduction of behavioural loss aversion was associated with decreased amygdala activity (Sokol-Hessner et al., 2013), suggesting that behavioural (as explained by a reduction in loss aversion with the regulate strategy) and neural (as indicated by the fMRI results and the difference which was associated with loss aversion) modulation of loss aversion can co-occur. Our study extends understanding of loss aversion by showing that, under certain conditions, loss aversion might be accompanied by a hindrance in the corresponding neural patterns, even without changes in its behavioural manifestation. This means that loss aversion was associated with neural activity under certain conditions only.

To conclude, we showed that loss aversion was not associated with feedback potentials unanimously, but rather, this association is subject to certain conditions. Specifically, in order for loss aversion to be associated with the evaluation of experienced decision outcomes, decision makers must be sensitive to having choice freedom and outcomes must be contingent upon their own choices.

Chapter 6

Study 4: Loss aversion is associated with the neural processing of decision outcomes only when making decisions impacting the self but not others.

This experiment investigated the effects of loss aversion on the neural evaluation of monetary rewards earned either for participants themselves or for another participant.

It is currently in preparation for publication in a journal to be confirmed.

6.1 Abstract

Behavioural studies suggest that loss aversion, the tendency to overestimate losses over gains, is reduced when deciding for others. Electroencephalography (EEG) studies have demonstrated that loss aversion is associated with feedback-related negativity (FRN), a component manifesting as stronger activity for negative compared to positive decision outcomes. Whether loss aversion is associated with FRN in a similar manner when decisions impact others remains to be explored. The present study aimed to compare the influence of loss aversion on the neural evaluation of monetary outcomes obtained by participants for themselves or for others using EEG recordings.

Participants completed a gambling task in which they could win or lose money for themselves (self-condition) or on behalf of another participant (other-condition). Parametric modelling of choices was used to estimate loss aversion separately in the self- and other-condition. Event-related potentials (ERPs) to outcomes in the self- and other-condition were analysed and correlated with loss aversion.

No statistically significant differences were found for loss aversion between the self- and the other-condition. The classic FRN was observed in the self-condition, with losses producing more negative amplitudes compared to gains. In contrast, FRN in the other-condition demonstrated the opposite pattern. Furthermore, loss aversion correlated with FRN in the self-condition only.

Results suggest that, despite participants deciding similarly for themselves and others at the behavioural level, decision outcomes obtained for themselves versus others were processed differently at the neural level. This may be reflective of a subconscious comparison between self- and other-outcomes, leading to the evaluation of others' gain as a relative loss for themselves.

6.2 Introduction

Making decisions on behalf of others might differ to the decisions made for oneself. Previous studies have highlighted self-other discrepancies in the context of risky decision making, with some studies suggesting that people make riskier decisions when deciding for others compared to when deciding for themselves (Chakravarty et al., 2011; Hsee and Weber, 1997; Pollai and Kirchler, 2012), although these findings are not conclusive (Fernandez-Duque and Wifall, 2007; Stone et al., 2002).

When decisions involve the prospect of a loss, people tend to overestimate losses compared to gains of the same nominal values, a phenomenon known as loss aversion (Kahneman and Tversky, 1979). Previous behavioural studies suggest that loss aversion is reduced when deciding for others compared to deciding for the self (Andersson et al., 2014). Furthermore, Fullbrunn et al. (2017) demonstrated that, when decision outcomes have joint implications for the self and for another person, loss aversion is of similar magnitude to when decisions impact only the self. Combined, the above findings support a general reduction in loss aversion when making decisions for others without consequences for the self.

Further support for the discrepancies in decision making for the self versus others is provided by neuroimaging studies. A meta-analysis of functional magnetic resonance imaging (fMRI) studies demonstrated that reward-related brain regions were activated for both personal and vicarious reward, while areas relevant for mentalising responded specifically to vicarious reward (Morelli et al., 2015). For instance, activation of the striatum has been shown to be dependent on whether the decision outcome leads to a reward for the self or to a reward for another participant (Braams et al., 2014). In particular, rewards won for the self or for a friend were associated with increased striatum activity compared to penalties, whereas the opposite pattern was found when outcomes concerned a disliked other. Likewise, reward-related brain regions have shown increased activation for decisions regarding the self, compared to decisions concerning others, both at the decision phase and during reward receipt (Jung et al., 2013).

Electroencephalography (EEG) studies have highlighted the importance of feedback-related negativity (FRN) in the neural processing of reward. FRN is an

event-related potential (ERP) component manifesting as a negative deflection in the electrocortical potential and differentiating between positive and negative outcomes (Gehring and Willoughby, 2002; Miltner et al., 1997). FRN occurs between 200 to 350 ms after feedback onset and displays a negativity over fronto-central scalp locations (Walsh and Anderson, 2012). Literature on observational feedback has demonstrated that watching rewards and penalties being delivered to others produces FRN that is of similar polarity to self-relevant rewards, albeit of smaller amplitude (Fukushima and Hiraki, 2009; Kang et al., 2010; Leng and Zhou, 2014; Ma et al., 2011; Yu and Zhou, 2006). In contrast, antagonistic situations where monetary rewards obtained for others translate into losses for the self lead to an opposite-polarity FRN (Fukushima and Hiraki, 2006; Itagaki and Katayama, 2008; Marco-Pallarés et al., 2010). However, in the above studies, participants passively observed outcomes being delivered to others and those outcomes were not dependent upon their own actions.

The effects of making active decisions for others on FRN have recently been investigated by Liu et al. (2018). Participants played a gambling game in three conditions; for themselves, for an underprivileged student (high-empathy condition) and for a student for whom no information was given (low-empathy condition). The classic FRN was observed in the self-condition, no differences between gain and loss amplitudes were found in the high-empathy condition, while an opposite-valence FRN was present in the low-empathy condition. These results suggest that evaluation of vicarious rewards is modulated by empathy levels. Crucially, in the above study, gains for others were associated with losses for the participant as the amount won for others was subtracted from participants' accumulated rewards. In another study, participants gambled for a friend or for a stranger and rewards won for the friend were associated with a stronger FRN compared to rewards won for a stranger, suggesting that FRN strength is modulated by social distance (Leng and Zhou, 2014).

FRN has previously been shown to be correlated with loss aversion when participants decided for themselves. Specifically, individual differences in loss aversion correlated with FRN strength in fronto-central electrode sites during 233-263 ms after learning the decision outcome (Kokmotou et al., 2017). Furthermore, this association between loss aversion and FRN has been shown to be specific only for decisions that had real but not hypothetical impact for participants (Kokmotou et al.,

under review). However, whether loss aversion modulates FRN in a similar manner when decisions impact others remains unknown.

The present study investigated the relationship between loss aversion and ERPs following monetary gains and losses resulting from decisions made by participants for themselves (self-condition) versus for another participant (other-condition). A gambling task was employed to evaluate loss aversion while EEG was recorded simultaneously. ERPs time-locked to outcome onset were computed separately for gain and loss outcomes for the self- and other-condition, and individual loss aversion values were correlated with FRN for each condition.

6.3 Methods

6.3.1 Participants

Twenty eight healthy participants (14 females) completed the study. One participant was excluded from the analysis due to a technical fault during the recording. Because the gambling task allowed participants to reject as many gambles as they wanted, nine more participants had to be excluded due to having less than 30 trials per condition, which is the recommended minimum number of trials necessary for FRN averaging (Huffmeijer et al., 2014; Marco-Pallarés et al., 2011). Therefore, the final sample included 18 participants (10 females), 2 left-handed, aged 24.39 ± 4.02 years (mean ± SD). The study was approved by the Research Ethics Committee of the University of Liverpool, and all participants gave their written informed consent prior to the start of the experiment.

6.3.2 Procedure

In order to estimate individual loss aversion values and to record EEG activity following decision outcomes, participants were asked to play a gambling task while connected to the EEG system. Specifically, participants received an initial endowment ranging between £9 to £11 to use for gambling during the task and were told that they could increase or decrease this amount depending on how well they performed throughout the experimental session. Participants were told that they would play this

gambling task once for themselves and once for the next participant lined up for the study. In the condition where participants gambled for themselves (self-condition), the outcomes of a randomly selected 10% from all trials would be given to them on top of their initial endowment as compensation for participating in the experiment. In the condition where participants gambled for the next participant (other-condition), they would keep nothing for themselves. Instead, the outcomes of a randomly selected 10% from all trials would become the next participant's endowment amount. Similarly, it was explained to participants that the endowment they received was won for them by the previous participant. However, unbeknownst to participants, the specific endowment amount was pre-selected before the start of the experiment. Specifically, this amount was a random number between £9-11 so that all participants received similar endowment amounts.

The gambling task was adjusted from previous studies (Kokmotou et al., 2017; Sokol-Hessner et al., 2009; Stancak et al., 2015) and the exact gamble amounts used and stimuli timing were identical to those described in detail previously (Kokmotou et al., 2017; Stancak et al., 2015). Figure 6.1 shows the trial structure. Participants were required to choose between a gamble and a sure outcome. The gamble offered 50% chance of winning or losing variable amounts of money (e.g., 'You win £3, You lose £3'). The alternative sure outcome was either zero or an amount smaller than the potential gain from the corresponding gamble in a particular trial. If participants accepted the gamble, feedback was given about whether they won or lost at that trial. Feedback constituted of the monetary amount in green colour with a '+' sign and red colour with a '-' sign for gains and losses, respectively. If participants rejected the gamble, they proceeded to the next trial.

Participants made a total of 200 choices for themselves and 200 choices for the next participant in separate blocks. The task was split into 4 blocks of 100 trials each with intervening breaks. The order of block type was counterbalanced across participants. Within each block, 80 trials consisted of choosing between a mixed-gamble (e.g., 'You win £3, You lose £3') and a sure zero outcome. The remaining 20 trials consisted of a gain-only gamble (e.g., 'You win £3, You lose £0') versus a sure non-zero outcome (e.g., £2). The inclusion of both mixed- and gain-only gambles enabled a dissociation of loss aversion from risk aversion as mixed-gambles assess loss aversion whereas gain-only gambles assess risk aversion (Sokol-Hessner et al., 2013). Similarly to previous studies (Sokol-Hessner et al., 2013), only mixed-gamble

trials were included in the ERP analysis in order to distinguish activity which was specifically relevant for loss aversion. It is not possible to assume that there is not a component of risk aversion in the decision to avoid a gamble, however, what this task does is to measure both loss and risk aversion and, by including the probability of a loss outcome in only one subset of the trials, then disentangle the two decision making parameters. The analysis conducted was similar to previous studies (Sokol-Hessner et al., 2009; 2013). As such, the advantage of this task is not that it assesses only loss aversion but rather that it separates it from risk aversion, as in the risk aversion trials there is no potential for loss.

Loss aversion was evaluated separately for the self- and other-condition, using parametric modelling of participants' choices based on prospect theory (Kahneman and Tversky, 1979). The exact gamble amounts used, value and logit functions, and numerical approximation method used have been reported in detail previously (Kokmotou et al., 2017; Stancak et al., 2015).

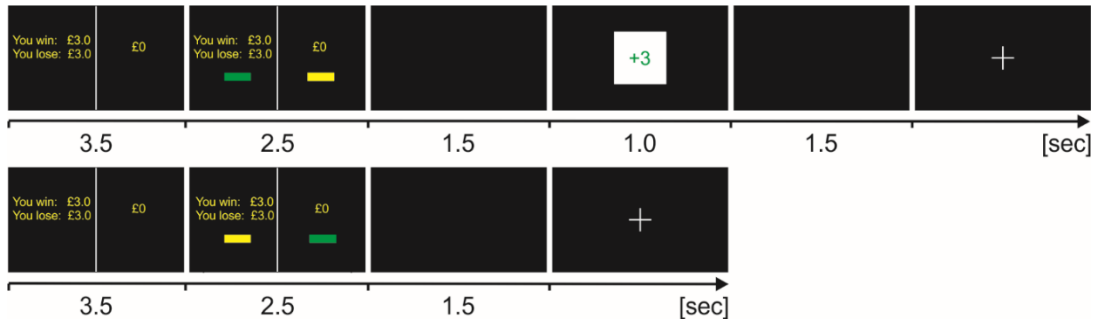

Figure 6.1. Trial structure of the loss aversion task. Each trial began with the presentation of two prospects, which stayed on the screen for 3.5 s. Half of the screen presented a gamble option offering 50% chance of winning or losing the displayed amount of money (e.g., 'You win £3.0, You lose £3.0'). The other half of the screen presented a sure outcome (e.g., £0). Next, two yellow rectangles appeared under each prospect and participants had 2.5 s to select the rectangle corresponding to the option they preferred by pressing the left or right mouse button. Their chosen rectangle turned green to highlight their choice and was followed by a 1.5 s black screen. Subsequently, if participants accepted the gamble (top panel), feedback was given about the gamble outcome. This feedback constituted of the monetary amount in green colour with a '+' sign or red colour with a '-' sign for gains and losses, respectively, and stayed on the screen for 1 s. One more 1 s black screen appeared before the start of the next trial. If participants chose the sure option (bottom panel), they proceeded to the next trial. The trial structure was identical for both self- and other-condition.

6.3.3 Recordings

EEG was recorded continuously throughout the experiment using a 129-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. The sensor net was aligned with respect to three anatomical landmarks; two preauricular points and the nasion. Electrode-to-skin impedances were kept below 50 kΩ, as recommended for this system (Ferree et al., 2001; Picton et al., 2000). The sampling rate was 1000 Hz and data were filtered online with a 0.01−200 Hz band-pass filter. The Cz electrode was used as the reference.

6.3.4 ERP analysis

EEG data were pre-processed using BESA v. 6.1 program (MEGIS GmbH, Germany). EEG signals were spatially transformed to reference-free data using the common average reference method (Lehmann, 1987). Eye blinks and electrocardiographic artifacts were removed by principal component analysis (Berg and Scherg, 1994). Data were also visually inspected for the presence of electrode artifacts due to muscle movement, and epochs contaminated with artifacts were excluded. Data were filtered from 0.5−35 Hz.

ERPs time-locked to feedback onset were computed separately for each of the four possible outcome conditions (self-gain, self-loss, other-gain, other-loss) resulting from the accepted mixed-gamble trials. Epochs from 200 ms before to 1000 ms after outcome onset were averaged for each condition and baseline-corrected using a time window of -200 to 0 ms relative to outcome feedback onset.

6.3.5 Statistical analysis

For statistical analysis, EEG data were exported to Matlab v. R2017a. Grand averaged ERPs from the four outcome feedback conditions were analysed with a two-way repeated measures ANOVA from 250 to 350 ms with decision type (self vs other) and outcome type (gain vs loss) as factors. The statistical significance was evaluated using permutation analysis (Maris and Oostenveld, 2007) with 5000 permutations in EEGLAB v.12 (Delorme and Makeig, 2004). Averaged data from time intervals

showing statistically significant effects were exported to SPSS Statistics software v. 22.0 (IBM Corp, 2013) for further analysis. Pearson's correlation analysis was used in order to investigate associations between loss aversion and ERPs.

6.4 Results

6.4.1 Loss aversion

Mean loss aversion for decisions regarding the self was 1.81 ± 0.20 (mean ± SEM) and loss aversion for decisions regarding others was 1.31 ± 0.16. A paired samples t-test showed that there were no statistically significant differences in loss aversion for decisions regarding the self versus others ($t(17) = 1.81$, $p = 0.088$), suggesting that participants decided in similar ways for themselves and others.

6.4.2 FRN

Figure 6.2A shows grand averaged ERP waveforms for the four possible feedback conditions (self-gain, self-loss, other-gain, other-loss) of the FRN electrode cluster (comprising electrodes FCz and Fz) on the left and their corresponding topographic maps on the right. To investigate the effects of decision and outcome type on FRN, a 2 (decision: self vs other) by 2 (outcome: gain vs loss) repeated measures ANOVA was conducted on data pooled over the FRN electrode cluster from 250-350 ms after feedback onset.

The ANOVA revealed a statistically significant interaction between decision and outcome type during 315 to 345 ms after feedback ($F(1,17) = 15.01$, $p < 0.05$). This time window is indicated by the light grey shaded area in Figure 6.2A. A paired samples t-test on mean data from this time window showed that, when participants were deciding for themselves, losses yielded more negative amplitudes compared to gains (losses: 3.55 ± 0.81 μV vs gains: 4.26 ± 0.77 μV; $t(17) = 3.29$, $p < 0.05$), revealing the classic FRN effect. When deciding for others, results showed the opposite pattern with losses being more positive compared to gains (losses: 2.48 ±

0.59 μV vs gains: 1.79 ± 0.45 μV; $t(17) = -2.20$, $p < 0.05$), suggesting that decisions regarding others yielded an opposite-direction FRN.

The main effect of decision was significant during 286 to 346 ms after feedback ($F(1,17) = 17.17$, $p < 0.05$). This time window is indicated by the dark grey shaded area in Figure 6.2A. A paired samples t-test on mean data from this time window showed that feedback following decisions for the self yielded stronger amplitudes compared to decisions for others (self-decision: 3.36 ± 0.70 μV vs other-decision: 1.73 ± 0.48 μV; $t(17) = 2.97$, $p < 0.05$). The main effect of outcome was not significant ($p > 0.05$).

6.4.3 Correlations with loss aversion

Pearson's correlation analysis was carried out to investigate the relationship between loss aversion and FRN following outcomes resulting from decisions for the self or for others during the time interval of the statistically significant interaction (315-345 ms). For decisions regarding the self, a difference waveform was created by subtracting ERPs to self-gains from ERPs to self-losses (self-FRN). For decisions regarding the self, a difference waveform was created by subtracting ERPs to other-gains from ERPs to other-losses (other-FRN).

Loss aversion for decisions regarding the self correlated with self-FRN ($r(18) = 0.57$, $p < 0.05$). Loss aversion for decisions regarding others did not correlate with other-FRN ($r(18) = 0.04$, $p > 0.05$). Figure 6.2B shows the scatter plots, regression lines and 95% confidence interval lines representing the associations of loss aversion with self-FRN (left) and other-FRN (right). The topographic maps of the two difference waveforms are also depicted in Figure 6.2B and 6.2C, where it is evident that self-FRN yielded a negativity over fronto-central scalp locations whereas other-FRN had the opposite pattern.

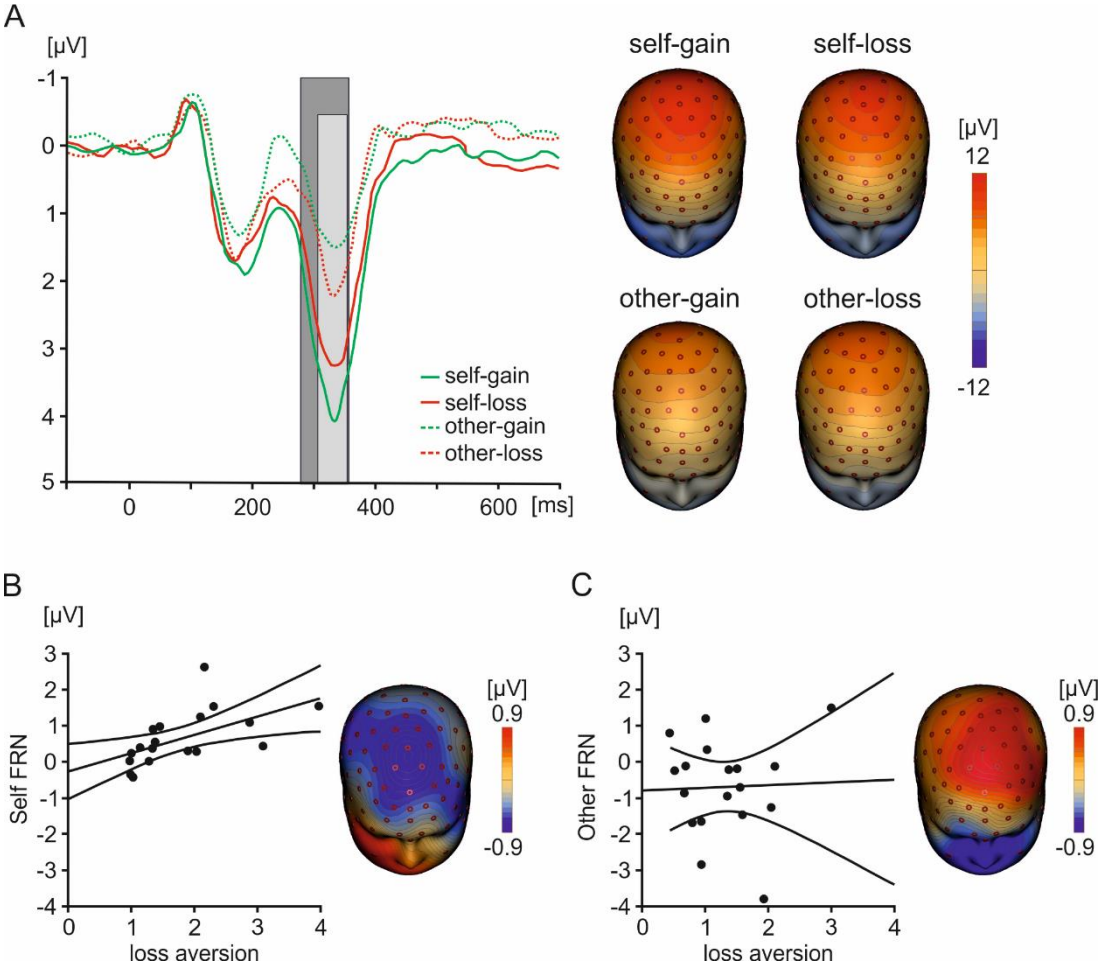

Figure 6.2. A. Grand averaged EEG potentials for the four feedback conditions (self-gain, self-loss, other-gain, other-loss) pooled over the FRN electrode cluster (FCz, Fz). The light grey shaded area corresponds to the time interval of the statistically significant interaction between decision and outcome type (315-345 ms). The dark grey shaded area corresponds to the time interval of the main effect of decision type (286-346 ms). Topographic maps of each feedback type are shown at the peak of the conditional waveforms (approximately at 320 ms). B. Scatterplot, linear regression line and 95% confidence interval lines representing the correlation between loss aversion and FRN in the self-condition with the corresponding topographic map shown at 320 ms. C. Scatterplot, linear regression line and 95% confidence interval lines representing the correlation between loss aversion and FRN in the other-condition with the corresponding topographic map shown at 320 ms.

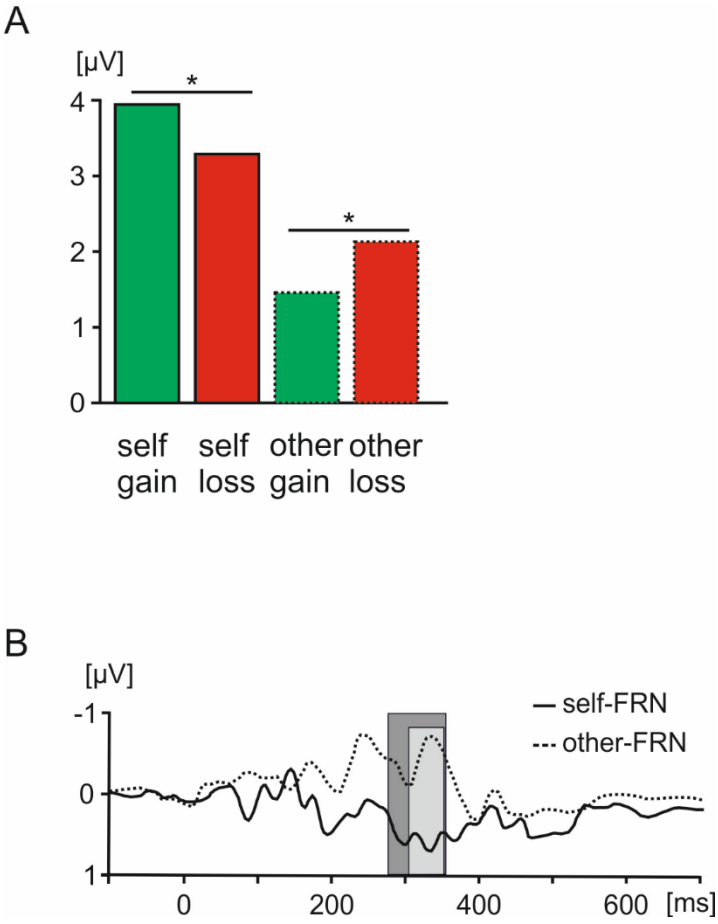

Figure 6.3. A. Mean EEG amplitudes for the four feedback conditions (self-gain, self-loss, other-gain, other-loss) pooled over the FRN electrode cluster (FCz, Fz) averaged over the time window of the statistically significant interaction (315-345 ms). B. FRN averaged potentials in the self-condition (solid black line) and other-condition (dashed black line). The light grey shaded area corresponds to the time interval of the statistically significant interaction between decision and outcome type (315-345 ms). The dark grey shaded area corresponds to the time interval of the main effect of decision type (286-346 ms).

6.5 Discussion

The present study investigated loss aversion and its influence on neural evaluation of outcomes during decisions impacting participants themselves versus others. Behavioural data showed that loss aversion did not differ between conditions, suggesting that participants were equally sensitive to prospective losses irrespective of whether those losses concerned themselves or others. However, decision outcomes for oneself or for another person appeared to be processed differently at the neural level. In the self-condition, the classic FRN component was observed with losses yielding more negative amplitudes compared to gains. In the other-condition, the inverse pattern was observed, leading to an opposite-polarity FRN effect, suggesting that gains (losses) for others were evaluated as losses (gains) for the self. Importantly, loss aversion was associated with FRN only in the self-condition.

The lack of loss aversion differences between conditions was somewhat surprising considering previous studies which found reduced loss aversion for decisions regarding others (Andersson et al., 2014; Füllbrunn and Luhan, 2017; Mengarelli et al., 2014; Polman, 2012b). One possible explanation for this discrepancy might be that the participants in the current study perceived similarities between themselves and the other person (e.g., student status). Psychological distance, and specifically the social aspect of it, that is, how different one considers another person to the self (Liberman et al., 2007), has been highlighted as an important factor during decision making (Polman and Emich, 2011; Trope and Liberman, 2010). For instance, the negative impact of losses is considered smaller for larger compared to shorter psychological distances (Malkoc and Zauberman, 2006). Importantly, Polman (2012b) showed that, in conditions of low psychological distance, decisions for others were similar to decisions regarding the self. Furthermore, smaller perceived psychological distance leads to a prevention focus, whereas larger is associated with a promotion focus (Trope and Liberman, 2010). Likewise, Polman (2012a) demonstrated an association between loss aversion and regulatory focus (Crowe and Higgins, 1997; Pennington and Roese, 2003) such that those with a promotion focus showed higher loss aversion for themselves versus others, whereas those with a prevention focus showed no differences. Therefore, if participants in the current study perceived small

psychological distance between themselves and the other participant, losses might have been equally aversive in both conditions.

6.5.1 FRN

In the self-condition, we observed the classic FRN component, with losses yielding more negative amplitudes compared to gains, thus, replicating many previous studies (Gehring and Willoughby, 2002; Nieuwenhuis et al., 2005c; Yeung and Sanfey, 2004). In the other-condition, we observed the opposite effect, suggesting that participants evaluated the gains (losses) of others as losses (gains) for the self. The finding of an opposite-FRN effect for decisions regarding others aligns with the low-empathy condition in the study by Liu et al. (2018) whereby the other person was a student similar to the participant. The authors observed an FRN of opposite polarity when participants did not feel empathy for the other person. Similarly, it is consistent with previous studies which demonstrated an opposite-polarity FRN in antagonistic situations during observational learning (Fukushima and Hiraki, 2006; Itagaki and Katayama, 2008; Marco-Pallarés et al., 2010). However, when personal and vicarious rewards were independent, observational FRN has been shown to be of the same polarity (Fukushima and Hiraki, 2009; Kang et al., 2010; Leng and Zhou, 2014; Ma et al., 2011; Yu and Zhou, 2006). Nevertheless, in the above observational learning studies, participants did not make active decisions for others, rather, they just observed the random delivery of rewards. In the current study, the rewards won for others were contingent upon participants' own actions, perhaps making the other person's outcomes more relevant and, thus, enhancing comparison effects between personal and vicarious rewards.

FRN has been shown to encode outcomes not in absolute but in relative ways (Holroyd et al., 2004) based on their motivational significance for participants (Gehring and Willoughby, 2002). For instance, it has been shown that when two gains of different size are possible but the smaller one is received, participants consider this as a relative loss (Holroyd et al., 2004). Similarly, a gain for others might have constituted a loss for the self since it signified a missed opportunity. Along those lines, Boksem et al. (2011) showed that FRN is dependent on social comparison. Specifically, FRN was modulated by another player's outcome during a gambling task

such that it was the most negative when the other player received positive feedback while other's negative feedback did not make any difference. This suggests that FRN was the most pronounced during the participant's comparison with a better performance than their own. Likewise, it has been shown that ventral striatum was activated similarly during both absolute and comparative rewards, such as when losing a specific amount or when winning an amount smaller than another participant (Dvash et al., 2010). Moreover, another study showed that people reported being envious when others' outcomes were better than their own, with more envy being associated with increased anterior cingulate cortex activity (Takahashi et al., 2009), a brain region which is considered a possible FRN source (Gehring and Willoughby, 2002). In general, upward comparisons lead to negative emotions (Dvash et al., 2010; Roese and Epstude, 2017; Wu et al., 2011; Zeelenberg et al., 1998) and it is these emotions that might have been reflected in the FRN response during learning the outcomes obtained for others.

6.5.2 FRN associations with loss aversion

The association between loss aversion and FRN strength in the self-condition replicates previous findings (Kokmotou et al., 2017). In particular, loss aversion measured during a separate task was associated with FRN amplitude recorded using a different forced-choice gambling task at fronto-central electrode sites during 233 to 263 ms after learning the choice outcome (Kokmotou et al., 2017). We postulate that, the more prospective negative outcomes were feared during the decision making process, as indicated by increased loss aversion, the more the brain differentiated between outcomes during the outcome receipt phase in the self-condition.

Previous studies have investigated the influence of loss aversion on ERPs. For instance, loss aversion has previously been associated with stronger resting state EEG activity in the right, compared to the left, hemisphere at central and posterior sites (Duke et al., 2018). Furthermore, loss aversion has been shown to modulate a posterior positive slow wave during difficult decisions, as indicated by small gain/loss ratios (Heeren et al., 2016). Additionally, fMRI studies provide evidence for a link between loss aversion and a range of brain regions which play an important role in value computation and evaluation of rewards, including the VMPFC, the amygdala and the

insula (Canessa et al., 2017; 2013; De Martino et al., 2010; Gelskov et al., 2015; Markett et al., 2016; Tom et al., 2007).

In our previous study (Kokmotou et al., under review), loss aversion was selectively associated with actual but not with counterfactual outcomes (i.e., outcomes resulting from accepted gambles versus hypothetical outcomes resulting from rejected gambles that could have been obtained, if the individual had decided differently). This suggests that outcomes should have motivational significance for participants in order for loss aversion to take effect. Similarly, in the current study, outcomes for others were less important for participants since they did not influence their own earnings. Therefore, although participants had a similar level of motivation to win for themselves and others, as indicated by the lack of differences in the behavioural results, loss aversion was not associated with others' outcome evaluation, namely FRN in the other-condition.

Taken together, the behavioural and EEG results suggest that there might have been a two-stage process taking place. Firstly, losses have been evaluated equally aversive during the decision time for participants themselves and others alike, leading to similar loss aversion values in both conditions. Secondly, an automatic involuntary evaluation of decision outcomes after they were received led to social comparisons between the rewards achieved for the self versus those for others. The lack of association between behavioural and neural data in the other-condition might indicate that the emotional responses associated with loss aversion at the time of the decision were diminished by the time participants learned the decision outcome. This is in line with literature proposing that decision making for the self compared to others recruits different neural evaluation mechanisms. For instance, one study showed that making decisions with negative consequences for the self was associated with regret, while making wrong decisions for others was associated with guilt and, importantly, regret led to stronger emotional reactions compared to guilt (Wagner et al., 2012). Furthermore, the emotional reactions experienced following risky decisions are not always of the intensity that they were hypothesised to be during deliberate thinking about those decisions (Loewenstein et al., 2001). Thus, the asymmetry in the neural evaluation of self-other outcomes might have been due to a mistaken initial hypothesis that participants would be gratified by another individual winning a reward in the same way that they would be gratified if they received the reward themselves.

To conclude, we showed that loss aversion during a monetary gambling task was similar for decisions made both for participants themselves and for others. However, the similarities in the amount of loss aversion revealed at decision time were not reproduced during the outcome evaluation period. In particular, the classic FRN component was observed for self-decisions, whereas an opposite-direction FRN was observed for other-decisions, suggesting differential processing of self- and other-outcomes. Finally, loss aversion was associated with FRN only when making decisions for the self but not when making decisions impacting others, further emphasising the observed discrepancies between behavioural and EEG data for participants themselves versus others.

Chapter 7

General Discussion

The overall aim of this thesis was to explore the effects of loss aversion on the evaluation of decision outcomes, and to investigate the neural mechanisms underlying such effects using EEG. It was hypothesised that individual differences in loss aversion would correlate with the neural evaluation of monetary decision outcomes, and that such modulation would be observed in feedback ERPs. Specific conditions influencing the loss aversion effects were identified by studying decision making in different contexts.

7.1 Summary of findings

The first study of this thesis investigated whether individual differences in loss aversion evaluated using a monetary gambling task were associated with FRN strength measured during a second forced-choice gambling task. It was hypothesised that people high in loss aversion would also show increased FRN. An exploratory SPM analysis showed that loss aversion was associated with FRN strength at fronto-central electrode locations during 233 to 263 ms after feedback onset. ERP analysis of the scalp data revealed the classic FRN with monetary losses yielding more negative amplitudes compared to gains. Correlation of behavioural loss aversion data with mean amplitude data from the 233-263 ms time window revealed statistical significance, suggesting that higher loss aversion values were associated with stronger FRN. Source analysis estimated that OFC was the generator of the FRN, and OFC activity strength during the 233-263 ms window was further associated with individual differences in loss aversion. Finally, a comparison analysis between loss and risk aversion showed that these findings were specific to loss aversion as risk aversion was associated both with different scalp topographic pattern and timing while it was not associated with FRN amplitudes.

The second study utilised a single gambling task with EEG recordings in order to simultaneously measure loss aversion and neural processing of both actual and counterfactual choice outcomes. The aim of this investigation was to replicate the correlational results from the first study and, furthermore, to explore the neural processing of counterfactual outcomes. It was hypothesised that individual differences in loss aversion would correlate with FRN strength following both actual and counterfactual outcomes. The findings from the first study were replicated such that loss aversion was associated with FRN following obtained gains and losses during 250-350 ms after feedback onset at fronto-central midline electrodes. In addition to FRN, scalp data suggested the presence of a P300 potential, so this component was also analysed. Results for P300 mirrored those of FRN, and loss aversion was associated with P300 strength during 350-450 ms at centro-parietal electrodes. However, contrary to our hypotheses, differences between ERPs following gains and losses were not statistically significant in the counterfactual outcome condition, while loss aversion was not associated with FRN or P300 to counterfactual outcomes. This result suggests that outcomes must have real economic consequences for individuals in order for loss aversion to influence the evaluation phase of the decision making process. After the exploratory analysis of the first study, this second experiment further supported associations of loss aversion with feedback ERPs and set a first condition for the loss aversion effects: outcomes must be of significance to the participants.

The third study aimed to investigate an important factor in decision making that has scarcely been investigated in EEG literature, namely, decisions when there are obstacles interfering with the choice process and outcome receipt. A modified FRN gambling task was used in tandem of real world limitations during decisions. It was shown that, following obstructed decisions, participants showed a decreased P300 component compared to when they were able to choose freely between alternative options. Following the receipt of outcomes, the classic FRN was observed for both choice conditions. A median split of the sample between participants showing strong and weak P300 amplitudes was used to investigate effects of individual differences in sensitivity to having choice freedom on outcome processing. Results showed that outcomes from choices made by participants themselves and outcomes resulting from arbitrary inflicting decisions upon participants were processed differently on the neural level. This effect was specific for losses such that losses resulting from

unchosen outcomes produced stronger amplitudes compared to those from decisions chosen by participants. This effect was not significant for gains. Furthermore, this result was only found for strong but not weak responders, suggesting that the latter did not focus on how outcomes were obtained but rather focused only on their valence. Crucially, loss aversion was associated with FRN only in the condition of outcomes freely chosen by participants and only for strong responders. Thus, this third study established further conditions for loss aversion to influence the neural processing of decision outcomes: participants must be sensitive to having choice freedom and outcomes must result from their own choices.

The fourth study investigated loss aversion within a social context. Specifically, this study aimed to investigate both behavioural differences in loss aversion for decisions regarding the self and decisions regarding others as well as the neural underpinnings of such decisions. Participants were led to think that they would be gambling to win money for themselves or for another participant. Results revealed that participants decided similarly for themselves and others on the behavioural level, as indicated by a lack of statistically significant differences between loss aversion in the self and the other condition. For decisions regarding the self, the classic FRN was found. Surprisingly, for decisions regarding others, the FRN was of opposite direction, suggesting that rewards gained for others were probably experienced as relative losses for the self on the neural level. This finding might have been due to a social comparison taking place between gains for the self versus gains for others leading to emotions of envy or disappointment. Furthermore, loss aversion correlated only with FRN following decisions about the self but not decisions about others, suggesting that loss aversion was a reliable predictor of outcome processing only when outcomes concerned the individual. These discrepancies between behavioural and neural data might suggest that, even though participants appeared to have been equally eager to win for themselves and others, rewards for others were not experienced similarly to rewards for themselves after learning the decision outcome. This final study further clarified that outcomes must be important for the self but not for others in order for loss aversion to influence their neural processing.

7.2 Themes

Several common themes emerged from the experimental findings in the present thesis. The overarching finding was that loss aversion is consistently associated with feedback ERPs when it comes to outcomes that are motivationally significant for individuals. Such effects were represented in a range of experimental conditions, using different types of decisions.

7.2.1 Loss aversion is associated with the processing of important outcomes

A common theme emerging from all four experiments is that loss aversion is associated with the neural processing of decision outcomes that are of motivational significance for the decision maker. Individual differences in loss aversion were associated with individual differences in FRN amplitude strength across all studies when decisions had monetary consequences for participants. In contrast, loss aversion was not associated with FRN when decisions did not have any monetary consequences for participants. Furthermore, loss aversion was not associated with FRN when participants were forced to receive a reward or penalty that was randomly selected for them by the computer.

These findings correspond to behavioural studies suggesting that the presence and magnitude of loss aversion depend on whether a future reward is deemed as worthy (Harinck et al., 2007) and whether the decision maker has the intention to pursue a specific outcome (Novemsky and Kahneman, 2005). The findings are also in line with literature showing that the motivational significance of a reward influences a range of decision making aspects, including the amount of mental (Boksem and Tops, 2008; Botvinick et al., 2009; Westbrook et al., 2013) and physical (Hartmann et al., 2013; Schmidt et al., 2012) effort dedicated towards achieving the reward, initial goal setting (Venables and Fairclough, 2009), attention paid to the task (Engelmann et al., 2009; Hübner and Schlösser, 2010; Padmala and Pessoa, 2011), and time spent looking at the reward (Krajbich et al., 2010; Libera and Chelazzi, 2006).

The finding that loss aversion consistently correlated with the processing of economically important outcomes extends these results and provides further evidence

that important and unimportant outcomes have differential effects on feedback-related cortical activity patterns. Likewise, a range of neuroimaging studies have manipulated the motivational significance of rewards by differentiating between monetary versus non-monetary incentives. For instance, larger FRN amplitudes were observed during incentive trials (e.g., where the participant received money for selecting the correct option) compared to non-incentive trials (e.g., where the participant received nothing or just points that did not translate into monetary rewards), and this effect appeared irrespective of whether incentives were defined in terms of earning rewards or avoiding penalties (Potts, 2011). Another study directly compared real and hypothetical rewards and found that real rewards led to stronger FRN and P300 amplitudes (Xu et al., 2018). Similarly, feedback about monetary rewards was associated with stronger FRN amplitudes compared to non-monetary feedback that merely signalled correctness (Van den Berg et al., 2012). Along those lines, an fMRI study found stronger OFC and VS activation when participants made real compared to hypothetical purchases (Kang et al., 2011).

The differences in the associations of loss aversion with feedback electrocortical potentials regarding important and unimportant outcomes can be understood within research frameworks suggesting that the neural representation of reward does not reflect a single aspect, but rather, the brain encodes information about (at least) two distinct aspects of outcomes, namely, their motivational and affective relevance (Carter et al., 2009). The motivational aspect refers to the value of the outcome (e.g., important versus unimportant), whereas the affective aspect refers to its valence (e.g., gains versus losses). For instance, one study manipulated both the motivational relevance of the reward (self- versus charity-directed rewards) and its affective relevance (gain versus loss), and found that activation strength within nucleus accumbens (NAcc) and ventral tegmental area (VTA) could be described as a function of reward magnitude during self-directed trials only, suggesting that activation in these brain regions primarily reflected the motivational relevance of the reward (Carter et al., 2009). The results from the current thesis extend this research by showing that loss aversion correlated with feedback ERPs exclusively in conditions of reward significance, while lack of self-relevance masked both loss aversion and valence associations, resulting in an attenuation of FRN amplitudes. Therefore, the distinction between important versus unimportant outcomes emerges as the most

significant factor for the association of loss aversion with feedback ERPs. This finding has important theoretical implications for loss aversion research, (i.e., that it is only associated with brain activity when the outcomes are important) while the present thesis further provides a step towards understanding when loss aversion plays a role during outcome processing by highlighting that not all outcomes are processed similarly, and, importantly, by identifying an initial set of specific conditions that need to hold in order for loss aversion to influence outcome evaluation.

7.2.2 Effects of individual differences on feedback ERPs

The results of the current thesis contribute to a more general literature on the role of individual differences in reward processing. Across all four experiments, individual differences in loss aversion were reflected in FRN amplitudes. A similar pattern of results was also found for the P300 potential in the second experiment. Given that both ERP components were computed as difference waveforms between gain and loss outcomes, these results appear to suggest that the more participants disliked the prospect of losing, the more the brain differentiated between positive and negative outcomes after those have been received. Furthermore, findings from the third experiment showed that individual differences measured on the neural level were associated with different electrocortical patterns during outcome evaluation. Specifically, participants who showed enhanced P300 amplitudes in response to having choice freedom, evaluated outcomes depending on how these outcomes were obtained, and this was seen as amplitude differences in loss ERPs between the two choice conditions.

Investigating the potential influence of individual differences during decision making is crucial for a better understanding of the cognitive processes associated with and leading to specific choice behaviours (Cohen, 2007). Given that loss aversion refers to the tendency to avoid negative consequences at the cost of obtaining positive ones, literature investigating individual differences in negativity bias can provide an explanatory context. For instance, increased subjective experience of negative affect and concern over the outcome of an event have been associated with stronger FRN (Santesso et al., 2008; Tucker et al., 2003). This finding is even more pronounced in research showing that depressed participants, compared to controls, exhibit enhanced

FRN amplitudes following negative feedback in the context of both incorrect performance (Tucker et al., 2003) and monetary loss (Santesso et al., 2008). Along those lines, it has been argued that the enhanced FRN amplitudes prevalent in individuals reporting high worry and anxiety relate specifically to an underlying negative emotionality (Hajcak et al., 2003).

Furthermore, negative affect is thought to be associated with individual differences in punishment sensitivity (Watson et al., 1999), which suggests that the FRN represents an enhanced neural response to penalties (Boksem et al., 2006). Previous studies have shown that individual differences in self-reported punishment and reward sensitivity are associated with FRN strength. Specifically, individuals high in punishment sensitivity produced enhanced FRN (Boksem et al., 2006), whereas those high in reward sensitivity produced attenuated FRN (Santesso et al., 2011). Punishment sensitivity was further associated with greater VMPFC activation during the FRN response (Amodio et al., 2008; Santesso et al., 2011). Furthermore, the increased FRN effect for individuals scoring high in punishment sensitivity was greater when negative feedback was associated with losing money compared to incorrect performance (Boksem et al., 2008). On the contrary, individuals high in sensation-seeking and reward sensitivity produced lower FRN following incorrect performance feedback (Cooper et al., 2014). Similarly, individuals who self-reported decreased motivation following negative feedback showed increased FRN amplitudes in a range of tasks (Santesso et al., 2008; Tucker et al., 2003), whereas individuals who self-reported stronger motivation after losing showed smaller FRN amplitudes (Segalowitz et al., 2011). Likewise, extraversion tendency (Campbell et al., 2003; Cohen et al., 2005) has been found to modulate FRN amplitudes such that highly extraverted individuals exhibited stronger FRN following unexpected rewards and smaller FRN following unexpected non-reward outcomes (Smillie et al., 2010).

It is evident from the above studies that negative emotionality plays an important role in the manifestation of FRN. The results of this thesis extend those findings by showing that the more sensitive an individual is to the prospect of negative consequences, the more distinctly the brain discriminates between positive and negative outcomes. Thus, understanding the role of individual differences in decision making and how these are mirrored on scalp data is an important factor that needs to be taken into account by decision making models and reward processing research more

generally. Towards this direction, the experiments described here focused on loss aversion as one decision making variable and its differences among participants and feedback ERPs differences in amplitude strength among participants as a reward processing variable. By demonstrating a robust association between loss aversion and FRN across the studies, we extend the previous literature described above investigating whether individual differences are associated with the amplitudes of individual ERP components.

7.2.3 Associations of decision utility with experienced utility

The effects of loss aversion measured during the decision making phase (i.e., when participants were contemplating among alternative outcomes) on the subsequent hedonic evaluation of those outcomes after the decision has been made can be understood in relation to research investigating how decision utility is related to experienced utility. Decision utility refers to the subjective expected value of an option at the time of choice, whereas experienced utility refers to the actual experienced hedonic value produced by the outcome at the time of consumption (Kahneman et al., 1997). Thus, decision utility at the time of choice would ideally lead to experienced utility at the time the decision is materialised. That is, when deciding, the goal is to receive a reward the hypothesised value of which is reflected on the decision utility. As such, by selecting the option that at the time of choice is valued as the most probable to lead to the highest reward, we expect this reward to be received and indeed be associated with an experienced utility as high as expected. Of course, this is not necessarily always the case as a mismatch between the two can lead to disappointment and regret and, potentially, a change in the decision strategy. Nevertheless, the reason for choosing a specific option is because the decision maker assumes or hopes that the chosen option will lead to the highest experienced utility.

The neural representations of decision utility have been investigated by reinforcement learning models, which associate predictive cues with their subsequent outcomes, under the assumption that cues indicating higher rewards will be preferred in subsequent choices after learning has occurred (O'Doherty, 2004; Schultz, 1997; Seymour et al., 2004; Sutton and Barto, 1998). Likewise, experienced utility and the

way the brain encodes signals associated with received rewards has been investigated by decision making studies under the general assumption that higher experienced utility will be associated with stronger activation in reward-related brain regions (Bayer and Glimcher, 2005; Delgado, 2007; Knutson and Greer, 2008; Kringelbach, 2005; Montague and Berns, 2002).

Although it is important to investigate the specific properties of decision and experienced utility separately, it is equally essential to investigate whether and how those two different types of utility are associated. Along those lines, individual differences in striatal activity during deciding whether to punish a player for an unfair offer during an economic game was associated with the amount of money that participants actually paid in order to punish that individual (De Quervain et al., 2004). Likewise, striatal activity during forced charity donations was associated with the amount of money participants donated to charities during voluntary donations (Harbaugh et al., 2007). Furthermore, it has been shown that stimulus cues that predict outcomes evoke an FRN even before the actual feedback is received, with a topographic pattern very similar to the one produced by feedback itself. In particular, cues that predicted future losses compared to gains produced stronger FRN and this effect was found both when cues signalled sure future losses (Dunning and Hajcak, 2007; Hajcak et al., 2007) and probable future losses (Holroyd et al., 2011; Liao et al., 2011; Walsh and Anderson, 2011). Importantly, individual differences in the endowment effect, which has been proposed to be a consequence of loss aversion (Kahneman et al., 1991), were correlated with the difference in striatal activity strength between buying and selling trials (De Martino et al., 2009).

These studies provide support for the notion that the value assigned to a future prospect at the time of the decision depends on a subjective estimation about the quality of the experience of that prospect (Kahneman and Snell, 1990). Along those lines, loss aversion has been interpreted as a predictive cognitive mechanism associated with the psychophysics of hedonic experience (Camerer, 2005). Findings from the current thesis appear to provide support for this hypothesis by suggesting that loss aversion regarding future prospects was associated with FRN strength following the receipt of these prospects. Nevertheless, this postulation needs to be interpreted with caution as loss aversion in the current thesis was only measured behaviourally in two out of the four studies, while in the remaining two, a single-trial analysis that

would allow direct associations between decision and expected utility was not possible because of the nature of the experimental design and the ERP components under consideration. Nonetheless, our results extend previous fMRI research utilising a similar experimental paradigm and associating loss aversion with amygdala activity strength for experienced outcomes (Sokol-Hessner et al., 2013).

7.3 Limitations

The primary limitation of the current thesis is that the methodology used was constrained to EEG. The use of fMRI, or combined EEG-fMRI, would have been useful to further investigate this topic and relate the timing of loss aversion with activation in specific brain regions. However, due to the fact that loss aversion appears to constitute only a small part of the decision making process, EEG was deemed as the most appropriate method to capture this phenomenon due to its excellent temporal resolution. Furthermore, at the start of the experiments discussed here, the gap in the literature was specifically the spatiotemporal aspects of loss aversion, while fMRI studies, albeit limited, already existed on loss aversion, pointing to structures such as the amygdala or the VS (Sokol-Hessner et al., 2013; Tom et al., 2007). The key finding regarding the spatiotemporal correlates of loss aversion that emerged from the experiments described in the current thesis was that individual differences in loss aversion are associated with two distinct ERP components which differentiate between monetary gains and losses and which occur after the outcome of a decision has been received. Specifically, individual differences in loss aversion were associated with early (around 300 ms) medio-frontal (i.e., FRN) and later (around 400 ms) posterior (i.e., P300) brain potential components.

Another obvious limitation, yet one that is often disregarded in research of this type, is that experimental participants were predominantly undergraduate and postgraduate students. Thus, findings might not be possible to generalise in different samples (Peterson, 2001). Including different samples would be helpful to investigate the presence of loss aversion in participants that often need to make risky decisions and encounter high stake losses, such as police officers. Similarly, cultural variability between participants in the current studies was small, therefore, results should be interpreted with caution until they have been replicated cross-culturally. Nevertheless,

given practical limitations associated mostly with time constraints, we focused on students as the most common method for data collection.

Finally, another limitation is that for loss aversion estimation we only used a gambling task. This particular task was deliberately chosen because it has been widely validated for loss aversion research (Sokol-Hessner et al., 2013; Tom et al., 2007), and allowed us to disentangle loss and risk aversion, which are often confounded, so that we could ensure that our results were specific to loss aversion (Sokol-Hessner et al., 2013). This behavioural analysis disentangling loss aversion from risk aversion was followed in all four studies presented in the current thesis, irrespective of whether one or two experimental tasks have been used. However, only the first study focused on the differences between brain activity corresponding to loss aversion versus brain activity corresponding to risk aversion. As mentioned in Chapter 1, the first experiment was an exploratory one for which a whole brain approach using SPM was utilised. The brain activity corresponding to individual differences in risk aversion was investigated in order to ensure that it was different to the brain activity associated with individual differences in loss aversion. The reason for which this analysis was not followed for the other studies was both methodological and theoretical. The methodological constraint was that the number of trials for risk aversion (approximately 80% less than the loss aversion trials) would not allow a robust averaging of ERPs. The theoretical motivation was that the main focus of the studies was primarily loss, rather than risk, aversion. It was loss aversion specifically for which the neuroimaging literature was limited, whereas risk aversion has been investigated more often using a variety of tasks (e.g., Kuhnen and Knutson, 2005; Wu et al., 2012). Further advantage of this task is that rewards had real monetary consequences for participants and, presumably, highlighted the impact of decisions more compared to a task of hypothetical nature. Nevertheless, it would have been interesting to ask participants to make other kinds of decisions, perhaps with different (non-monetary) stakes.

7.4 Future research

One interesting possibility for future research would be to investigate loss aversion and/or FRN in clinical samples. Two general variables of the present thesis,

namely, decision making and reward processing, are also components whose dysfunction has been highlighted in several disorders. For instance, loss aversion is generally a negative/prevention mind-set that prevails in disorders such as depression or obsessive compulsive disorder (Pammi et al., 2015; Sip et al., 2018). Furthermore, feedback processing in the range of FRN in disorders such as schizophrenia is not yet fully understood. Therefore, investigating the status of these variables in clinical samples might further our understanding of the impaired cognitive and emotional information processing associated with particular decision making deficits, which could subsequently be targeted by specific interventions (e.g., cognitive behavioural therapy focusing on avoidance behaviours occurring due to an asymmetric evaluation of positive and negative/feared consequences).

Future studies could endeavour to use more realistic experimental paradigms. For instance, the use of EEG in combination with simultaneous eye tracking recordings during a real card game with two participants would be a possible scenario in order to extend the current findings in a more naturalistic setting. During the paradigms presented here, and as is common with most research of this nature, participants viewed stimuli on a computer screen, the order and timing of stimuli were strictly controlled and set in advance, and the entire task was generally very constrained. Even though these experimental settings were deliberately chosen in order to facilitate the collection of clean data and to ensure that ERP responses were time-locked to specific events, it would be interesting to see whether these findings hold when the experimental paradigm moves away from the experimenter's control.

Furthermore, the use of single-trial analysis techniques might be an interesting way to investigate specific neural activity alterations during reward processing. Ultimately, every day decision making is often a one-shot single decision process and not repetitive as is the case with the large number of trials necessary for creating grand averaged ERPs. Although it is generally considered a difficult challenge to use single-trial analysis with EEG data, it would be definitely useful for seeing how different monetary amounts influence loss aversion and FRN. For instance, we did not include reward magnitude as a factor in the current experiments because of the above described difficulties and also because previous research has suggested that reward magnitude is not encoded by FRN (Hajcak et al., 2006). Nevertheless, reward

magnitude changes from trial to trial might influence later components and future studies should try to incorporate this variable into a single-trial study design.

Another possibility would be to further investigate risk aversion and how it compares to loss aversion. Even though we made an initial step with the first study towards that direction, risk aversion was not the primary focus of the present thesis. Particularly, given the limited number of risk aversion trials in the current experiments, we were not able to investigate associations with brain data in detail. However, given that risk and loss aversion can co-occur and are often confounded in decision making research (Sokol-Hessner et al., 2013), it would be useful if future studies could disentangle their brain dynamics.

7.5 Concluding remarks

To conclude, this thesis employed risky decision making tasks and EEG recordings to investigate the neural mechanisms underlying loss aversion during the processing of decision outcomes. The results point towards an association between individual differences in loss aversion and FRN amplitude strength. This pattern was replicated across four studies, while at the same time a number of exceptions were highlighted. It appears that an important condition for loss aversion to influence the evaluation of decision outcomes is that these outcomes must be of motivational significance for the decision maker. Motivational significance in the present thesis was investigated in terms of counterfactual thinking (hypothetical outcomes that could have been obtained if the individual had decided differently), choice freedom (outcomes resulting from free choices compared to outcomes arbitrarily inflicted upon the individual), and, finally, social context (outcomes affecting others but not the decision maker). We showed that loss aversion is associated with FRN (study 1), but only when decisions have real economic consequences for individuals (study 2), when those consequences stem from individuals' free choices (study 3), and when the receiver of the reward are the individuals themselves (study 4). Results from the current thesis add to the growing literature on the neural underpinnings of loss aversion and decision making in general. Additionally, they expand previous findings on FRN literature and neural processing of rewards by suggesting that individual differences in decision making influence such processing. It is hoped that the findings will be

useful in future neuroimaging research addressing the effects of individual differences in decision making on cortical activity patterns, and the corresponding representation of reward processing in the brain.

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