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Fear-induced increases in loss aversion are linked to increased neural negative-value coding

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Abstract

Human decisions are often influenced by emotions. An economically relevant example is the role of fear in generating loss aversion. Previous research implicates the amygdala as a key brain structure in the experience of fear and loss aversion. The neural mechanism behind emotional influences on loss aversion is, however, unclear. To address this, we measured brain activation with functional magnetic resonance imaging (fMRI) while participants made decisions about monetary gambles after viewing fearful or neutral faces. We observed that loss aversion following the presentation of neutral faces was mainly predicted by greater *deactivations* for prospective losses (relative to *activations* for prospective gains) in several brain regions, including the amygdala. By contrast, increases in loss aversion following the presentation of fearful faces were mainly predicted by greater *activations* for prospective losses. These findings suggest a fear-induced shift from positive to negative value coding that reflects a context-dependent involvement of distinct valuation processes.

Key words: amygdala; value; emotion; loss aversion; decision making; psychopathy

Introduction

Human decisions are often guided by emotions (Phelps *et al.*, 2014; Lerner *et al.*, 2015). For example, financial investors may become gripped with fear during a stock market downturn and choose to sell their portfolios—an effect that is supported by experimental evidence (Cohn *et al.*, 2015). In this scenario, the emotion is related to the decision—fear is evoked by the prospective loss of stock value. However, even emotions that are

unrelated to the decision at hand, so-called incidental emotions, have been found to influence decision making (Schulreich *et al.*, 2014; Lerner *et al.*, 2015). For example, in financial decision making, changes in loss aversion in response to incidental emotions have been observed (Schulreich *et al.*, 2016).

Loss aversion refers to decision behavior characterized by a greater sensitivity to prospective losses than to prospective gains of equal size (Kahneman and Tversky, 1979). It is a component

of decision making that may be particularly prone to emotional influences. In a previous behavioral study, we found that incidental fear cues (images of fearful faces) presented before or during a lottery choice increased monetary loss aversion (Schulreich *et al.,* 2016). At the neural level, it remains unclear, however, *in which brain region(s)* and *through which mechanisms* this emotional effect on choice is mediated.

Regarding the brain region(s) involved, the amygdala is a key structure in the human brain that has been implicated in both affective processing and loss aversion. For instance, it is well established that the amygdala is critical for fear and threat processing (Tovote *et al.,* 2015). At the same time, amygdala-lesioned patients did not exhibit loss aversion, while matched controls did (De Martino *et al.,* 2010). This suggests that the amygdala plays a causal role in the generation of loss aversion. Given the described functional overlap, the amygdala is a plausible candidate for mediating the effects of incidental emotions on loss aversion.

Regarding the neural mechanisms involved, different valuation processes identified in previous research may play a role. To begin with, two types of loss signals have been associated with distinguishable, but at least partially overlapping, motivational systems (Brooks and Berns, 2013; Seymour *et al.,* 2015). The first type of system codes positive value via reward-related *activations* in a mesocorticolimbic circuit that includes the striatum (Bartra *et al.,* 2013; Brooks and Berns, 2013; Seymour *et al.,* 2015). Within this system, increasing losses are coded as *reductions* in neuronal activity (in other words, decreasing losses are coded as increases in neuronal activity). These responses have been observed for both prospective and experienced outcomes. Greater *deactivations* for increasing prospective losses relative to *activations* for increasing prospective gains—a feature termed 'neural loss aversion' in functional magnetic resonance imaging (fMRI) research—predict behavioral loss aversion (Tom *et al.,* 2007; Canessa *et al.,* 2013). In line with these researchers, we use the terms activations *and* deactivations to refer to a positive and negative slope of the BOLD response with respect to the loss or gain magnitude, and not as increased or decreased brain activity relative to some baseline condition. The second type of system codes negative value by generating loss signals via increasing activity in response to increasing losses—and also includes the striatum (Brooks and Berns, 2013; Seymour *et al.,* 2015). Notably, two studies found *activations* for prospective losses in the amygdala which also predicted behavioral loss aversion (Canessa *et al.,* 2013; Sokol-Hessner *et al.,* 2013)—implicating the amygdala's involvement with this second system. However, other studies observed stronger amygdala *deactivations* for prospective losses relative to gain-related activations (i.e. 'neural loss aversion'; Pammi *et al.,* 2017)—implicating the amygdala's involvement with the first system—or failed to find any loss-related amygdala activity (Tom *et al.,* 2007; Gelskov *et al.,* 2015). Reconciling these seemingly contradictory findings with each other, electrophysiological and optogenetic studies (in rodents) have demonstrated both activation-based and deactivation-based loss signals in the amygdala (Shabel and Janak, 2009; Beyeler *et al.,* 2016). Thus, the amygdala seems to play a role in both systems. However, the amygdalar mechanisms that generate loss aversion are still far from clear, especially with respect to the induction of loss aversion by negative emotions.

What is known about emotion-induced changes in these neural valuation mechanisms? Only two studies have investigated the influence of incidental emotions on loss aversion at the neural level (Engelmann *et al.,* 2015; Charpentier *et al.,* 2016). Neither of them reported value-related amygdala activity that

predicted emotion-induced changes in loss aversion. However, one of these studies found that enhanced amygdalar–striatal connectivity predicted increases in loss aversion following the presentation of fearful and happy compared to neutral faces (Charpentier *et al.,* 2016). The second study compared decisions under threat-of-shock and in a neutral context (Engelmann *et al.,* 2015). Surprisingly, the degree of behavioral loss aversion was not changed by threat-of-shock. However, choice behavior was predicted by brain activity in a context-dependent manner. Specifically, increasing activity for increasing subjective expected value—that is, *positive*-value coding—in the striatum and the ventromedial prefrontal cortex (vmPFC) positively predicted gamble acceptance in the neutral context. In contrast to this, increasing insula activity for decreasing subjective expected value—that is, *negative*-value coding—negatively predicted gamble acceptance in the threat-of-shock context. Since prospective losses contribute to expected value (together with prospective gains), greater loss-related activations are one possible source of the observed shift toward negative-value coding. This possibility, however, has not been explored thus far; for example, in the threat-of-shock study, brain activity was only regressed on subjective expected value, but not on its components—losses and gains—separately.

Given the prominent role that the amygdala plays in fear processing (Tovote *et al.,* 2015) and based on evidence for loss-related activations in the amygdala (Basten *et al.,* 2010; Canessa *et al.,* 2013; Sokol-Hessner *et al.,* 2013), we hypothesized that fear-induced changes in loss-related activations in amygdala activity could account for increases in loss aversion. More generally, the amygdala might be part of a broader, distributed network that displays a fear-induced shift from positive to negative value coding. Such a network might also include the striatum, vmPFC and insula (Engelmann *et al.,* 2015). We therefore investigated whether such effects explain fear-induced increases in monetary loss aversion.

Alternatively, changes in loss aversion might stem from changes of activity within a positive-value coding mechanism via enhanced deactivations for losses relative to activations for gains. Greater deactivations for losses than activations for gains—so-called 'neural loss aversion'—have been observed previously, for instance, in the striatum (Tom *et al.,* 2007; Canessa *et al.,* 2013).

In both cases, the emotional impact on neural value responses might result from a spillover of activity due to the processing of the preceding emotional cue on subsequent decision-related activity. Fear-related spillover effects have been observed previously, for example, from amygdala responses to fearful movies on subsequent activation to unrelated threat-signaling stimuli (Pichon *et al.,* 2015).

To test these hypotheses, we let participants perform a decision-making task (adapted from Schulreich *et al.,* 2016) while they were in the MRI scanner: participants decided to accept or reject gambles consisting of both a prospective gain and a prospective loss. To manipulate affect, we briefly presented images of fearful or neutral faces (Ebner et al., 2010) before each lottery choice (for more information on the task and affective priming, see Figure 1 and Supplementary Methods S1–S3). We chose fearful faces as emotional primes because they signal potential threats and reliably enhance amygdala activity (Fusar-Poli *et al.,* 2009). In line with previous studies (Tom *et al.,* 2007; Canessa *et al.,* 2013; Charpentier *et al.,* 2016), we separately analyzed neural responses to prospective losses and prospective gains in order to identify the exact mechanisms underlying fear-induced changes in valuation.
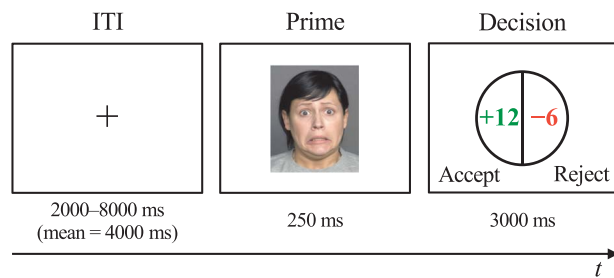
ITI	Prime	Decision

+

2000–8000 ms
(mean = 4000 ms)

250 ms

+12 −6

Accept   Reject

3000 ms

→ *t*

Fig. 1. Trial sequence. In each trial, an image of a face (fearful or neutral) was presented prior to a mixed gamble (within-subject design with 2 × 64 face-gamble trials). The priming procedure was embedded in a gender discrimination task (for more details see Supplementary Methods S1–S3). Mixed gambles included prospective gains and losses ranging from ±€6 to ±€20 in steps of €2 (8 × 8 = 64 gambles per condition, also see Figure 2A), and in all gambles, the two prospective payoffs had identical probability (i.e. 50%). Each participant received an initial endowment of €20, and the lotteries' gains/losses were added to/subtracted from this endowment if a given lottery was randomly chosen for final payment (random incentive mechanism); rejection of a gamble amounted to choosing the status quo (±€0). To ensure that intentionally missing a trial made no sense, participants were instructed that they would pay a penalty of €1 if a missed trial was randomly selected for the final payment.

Methods

Participants

We recruited 30 participants at Freie Universität Berlin and other local universities via flyers, mailing lists and social media. All participants were right-handed, had normal or corrected-to-normal vision and were screened for fMRI eligibility. Three subjects had to be excluded from the analysis: one was excluded because the subject did not understand the rules of the task (as assessed by a questionnaire) and two were excluded because they rejected all or nearly all lotteries, which made the parameter estimation in our behavioral modeling unreliable. Hence, the final analysis sample consisted of 27 participants [15 female; mean age 21.81 years (SD = 3.55 years)]. All participants gave written informed consent prior to the experiment, and the ethics committee at Freie Universität Berlin approved all procedures.

Behavioral modeling

We set up a two-parameter model—based on Prospect Theory's subjective-value function (Kahneman and Tversky, 1979)—in MATLAB (v. R2013a; The MathWorks, Inc.). Specifically, we assessed behavioral sensitivity to gains and losses by fitting a logistic regression with a piecewise-linear value function per condition. This allowed us to estimate each participant's loss aversion parameter λ and decision noise parameter σ and their change from the neutral-face to the fearful-face condition, $\Delta\lambda$ and $\Delta\sigma$, respectively (for more details, see Supplementary Methods S4). A value of $\lambda > 1$ indicates that the participant is loss-averse, $\lambda = 1$ indicates that the participant weighs gains and losses equally, and $\lambda < 1$ indicates that the subject weighs gains more strongly than losses. Comparisons of model-derived loss-aversion parameters (see Results section) as well as complementary analyses of choice frequencies, decision noise and response times (Supplementary Results S1–S4) were performed in SPSS (v. 22; IBM Inc.). In an exploratory analysis, we also investigated associations of behavior (and neural data) with personality traits reflecting (subclinical) variations in psychopathy (Supplementary Methods S5 and Supplementary Results S5). Missed trials were discarded from these analyses (13, or 0.38%, of all 3456 trials; only 8 participants missed any trial at all, and none of

them missed more than 3 out of 128 trials). All statistical tests were two-tailed, unless specifically stated otherwise.

fMRI data analysis

We acquired functional T_2^*-weighted gradient-echo-planar images and structural T_1-weighted images, using a 3 Tesla Siemens Magnetom Trio scanner and a 12-channel head coil. For more details regarding MRI data acquisition, see Supplementary Methods S6.

Data were preprocessed (Supplementary Methods S7 and S8) and analyzed using FMRIB's Software Library (FSL, v. 5.0.7; Jenkinson *et al.*, 2012) on the high-performance computing system at Freie Universität Berlin. Statistical time series analyses were performed using FMRIB's Improved Linear Model with local autocorrelation correction. We used a single general linear model (GLM) to analyze the entire neuroimaging dataset of each participant. In other words, we analyzed the neutral-face and the fearful-face condition jointly. Our GLM comprised nine task-related regressors and their temporal derivatives, denoting: (i) face-gamble trials per condition ($\beta_{gamble, neutral}$ and $\beta_{gamble, fearful}$), (ii) parametric modulators representing prospective gains (in euros; 6, 8, ..., 20) per condition ($\beta_{gain, neutral}$ and $\beta_{gain, fearful}$), (iii) parametric modulators representing prospective losses (in euros; *positively* coded, i.e. 6, 8, ..., 20) per condition ($\beta_{loss, neutral}$ and $\beta_{loss, fearful}$), (iv) gender recognition trials per condition and (v) missed trials.

Each regressor was a boxcar regressor, convolved with a double-gamma hemodynamic response function. The onset (and duration) of each regressor was aligned with the onset (and duration) of the event of interest. In particular, the face-gamble regressors ($\beta_{gamble, neutral}$ and $\beta_{gamble, fearful}$) were aligned with the onset of the display of the face picture. We chose to model each brief face presentation and the following gamble presentation as one event. This is because the two stages have to be so close in time—an important factor of affective priming to work (Hermans *et al.*, 2001)—that they cannot be clearly separated in fMRI data analysis, given the sluggish hemodynamic response. The four parametric regressors for the prospective gains and losses ($\beta_{gain, neutral}$, $\beta_{gain, fearful}$, $\beta_{loss, neutral}$ and $\beta_{loss, fearful}$) were aligned with the onset of the gamble that participants faced in the respective trial and thus with the onset of valuation processes.

Statistical inference was performed with higher-level mixed-effects (FLAME 1 and 2) comparisons (one-sided *t*-tests) of the first-level contrasts representing the face-gamble onsets and parametric regressors per condition. Our group-level analysis was informed by behavioral modeling, as we included both loss aversion (λ) and decision noise (σ) as covariates. Specifically, we estimated two models: (i) a model to investigate whether decision-related brain activity predicted baseline loss aversion ($\lambda_{neutral}$) in the neutral condition, controlling for baseline decision noise ($\sigma_{neutral}$), and (ii) a model to investigate whether fear-induced changes in decision-related brain activity predicted fear-induced changes in loss aversion ($\lambda_{fearful} - \lambda_{neutral}$), controlling for changes in decision noise ($\sigma_{fearful} - \sigma_{neutral}$). Our rationale for including decision noise was two-fold. First, previous studies found that decision noise is related to neural activity (e.g. Grueschow *et al.*, 2015; Kurtz-David *et al.*, 2019) and neurochemistry (Jocham *et al.*, 2012) in brain areas commonly attributed to valuation processes such as the vmPFC and striatum, which are also key areas in our study. Second, we found that degrees of loss aversion (and changes in loss aversion) were trend-wise significantly correlated with (changes in) decision noise in our data (see Supplementary Results S3). Hence, accounting for decision
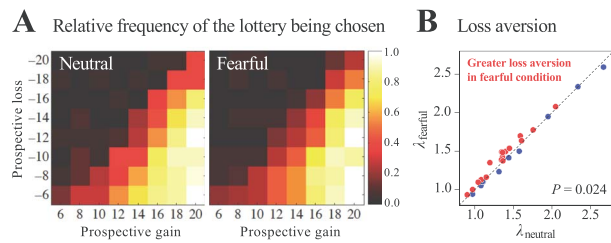
Fig. 2. Behavioral results. (**A**) Relative frequencies of the lottery being chosen in the two conditions across gain-loss combinations. Choice frequencies below 50% around the diagonal indicate loss aversion. On average, participants accepted slightly less gambles in the fearful-face condition (30.79%, SD = 13.66%) than in the neutral-face condition (31.81%, SD = 13.92%; for a statistical comparison, see Supplementary Results S1). (**B**) Estimates of the degree of loss aversion, λ, per condition. Red data points above the 45° line indicate greater loss aversion in the fearful-face condition (18 out of 27 participants, i.e. 66.67%); blue data points indicate no change or decreased loss aversion. On average, participants were significantly more loss-averse in the fearful-face ($\lambda_{\text{fearful}} = 1.46$, SD = 0.41) compared to the neutral-face condition ($\lambda_{\text{neutral}} = 1.43$, SD = 0.42).

noise may allow for a better assessment of processes unique to loss aversion. Importantly, effects for loss aversion remained qualitatively identical when not controlling for decision noise, as illustrated by the significant (simple) correlations between loss aversion and brain activity (see Supplementary Figure S1). As an additional check, we also ran single-covariate models—that is, we included only (changes in) loss aversion as a group-level covariate—and detected clusters that are highly similar to those in our main model.

For the region of interest (ROI) analysis, a false-discovery rate (FDR) correction with $P < 0.05$ and a minimum cluster extent of 10 voxels ($k \geq 10$) was applied. For details on the construction of our ROI mask, see Supplementary Methods S9. In our whole-brain analysis, we used a cluster-defining threshold of uncorrected $P < 0.001$ (i.e. $Z > 3.1$) and a family wise error cluster correction with $P < 0.05$.

All figures depicting BOLD parameter estimates are only included for illustrative purposes, with the exception of the scatterplots depicting the simple relationship (i.e. not controlling for decision noise) between (changes in) loss aversion and brain activity (see Supplementary Figure S1). At that point, we also report significance tests on the correlation coefficients, to demonstrate that within these clusters, a systematic relation between brain activation and behavioral loss aversion is also present according to the simpler model.

Results

Estimation of the degree of loss aversion in the neutral-face and fearful-face condition

Within the framework of prospect theory, loss aversion is a major source of risk aversion for mixed gambles (Wakker, 2010). We used quantitative behavioral modeling to investigate fear-induced changes in loss aversion (for more details, see Supplementary Methods S4). In particular, we estimated each subject's degree of loss aversion, λ, and its change between the two conditions. Importantly, unlike simply calculating choice frequencies (see Figure 2A and Supplementary Results S1), this method also assesses how noisy subjects' choices are (via a Fechner noise parameter, σ, see Supplementary Results S3). A parameter value $\lambda = 1$ indicates loss neutrality, while $\lambda > 1$ indicates loss aversion, and $\lambda < 1$ indicates gain seeking.

In the neutral-face condition, participants were on average loss-averse, $\lambda_{\text{neutral}} = 1.43$ (SD = 0.42), $t(26) = 5.225$, $P < 0.001$, $d = 1.024$. Critically, incidental fear cues slightly but significantly increased loss aversion when compared to the neutral-face condition, $\lambda_{\text{fearful}} = 1.46$ (SD = 0.41), $t(26) = 2.401$, $P = 0.024$, $d = 0.149$ (Figure 2B). Fear-induced changes in loss aversion did not depend on the degree of baseline loss aversion (Supplementary Results S2).
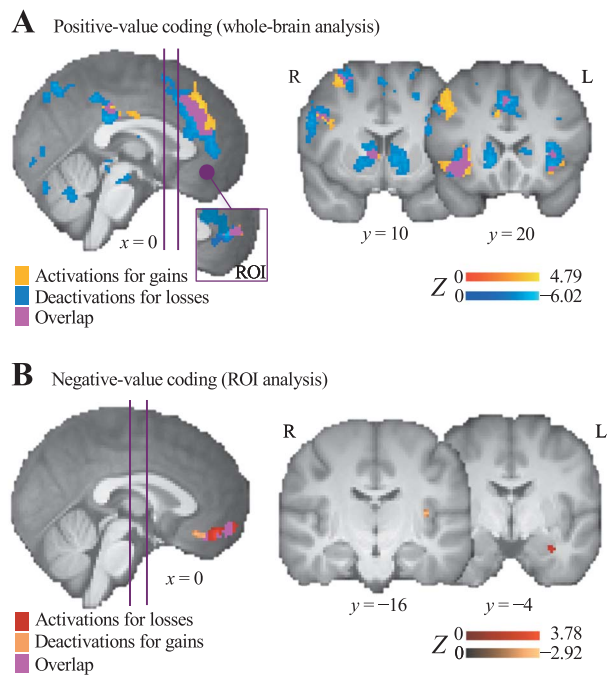
Neural responses to prospective gains and losses in the neutral-face condition

In the presentation of our neuroimaging results, we first focus on neural activity in the neutral-face condition, that is, in the absence of incidental fear cues. Along with a whole-brain analysis, we investigated the amygdala as an *a priori* ROI, given its abovementioned role in emotion processing (Tovote *et al.*, 2015) and loss aversion (De Martino *et al.*, 2010; Canessa *et al.*, 2013; Charpentier *et al.*, 2016). We also examined the striatum, vmPFC and insula as ROIs, given their role in (context-dependent) valuation (Bartra *et al.*, 2013; Engelmann *et al.*, 2015).

Let us first consider how prospective gains and losses modulate brain activation. Consistent with previous research (Tom *et al.*, 2007; Canessa *et al.*, 2013; Charpentier *et al.*, 2016; Pammi *et al.*, 2017), we observed partially overlapping sets of positive-value coding regions that showed activation that increases with the magnitude of prospective gains ($\beta_{\text{gain, neutral}} > 0$) or deactivations that become more negative with the magnitude of prospective losses ($\beta_{\text{loss, neutral}} < 0$) in the neutral-face condition. These regions include the bilateral striatum, ventral tegmental area, dorsal anterior cingulate cortex, anterior insula, paracingulate gyrus and rostral ACC/vmPFC, among others (Figure 3A and Supplementary Table S1 for ROI-based and S2 for whole-brain results). We also observed negative-value coding in certain regions in the neutral-face condition. Specifically, we found *activations* for prospective losses ($\beta_{\text{loss, neutral}} > 0$) and *deactivations* for prospective gains ($\beta_{\text{gain, neutral}} < 0$) in the medial orbitofrontal cortex (mOFC)/vmPFC, as well as activations for prospective losses in the left basolateral amygdala and deactivations for prospective gains in the left posterior insula (Figure 3B and Supplementary Table S1 for ROI-based results).

In addition, we replicated a pattern previously termed 'neural loss aversion' (Tom *et al.*, 2007), which is characterized by positive-value coding with greater deactivations for losses relative to activations for gains ($-\beta_{\text{loss, neutral}} - \beta_{\text{gain, neutral}} > 0$), in the neutral-face condition. To note, we compared the slope of deactivations for losses to the slope for activations for gains by flipping the sign of the loss regressor, as was done by Tom and colleagues (Tom *et al.*, 2007). If we did not flip the sign of the loss regressor—that is, if we computed $\beta_{\text{loss, neutral}} - \beta_{\text{gain, neutral}} > 0$—the contrast would instead test whether activations for losses were greater than activations for gains. We observed 'neural loss aversion' in regions such as the striatum, anterior insula and frontal medial cortex (Figure 4A and B and Supplementary Tables S1 and S2).

Next, we report how neural value responses are related to behavioral loss aversion. As a reminder, we included λ_{neutral} as a covariate in our fMRI group-level analysis, controlling for decision noise, σ_{neutral} (see Methods). Here, we observed that more loss-averse participants displayed greater 'neural loss aversion' (Supplementary Table S1), for example, in the left caudate (Figure 4A). This was mainly due to increasing deactivations for losses with increasing behavioral loss aversion (Figure 4C and Supplementary Tables S1 and S2). We also found that monetary loss aversion was positively associated with

Fig. 3. Neural responses to prospective gains and losses in the neutral-face condition. **(A)** Positive-value coding: activations for prospective gains ($\beta_{gain,\,neutral} > 0$) and deactivations for prospective losses ($\beta_{loss,\,neutral} < 0$) (whole-brain analysis; cluster-corrected with $Z > 3.1$ and $P < 0.05$). Here, we depict whole-brain results because they largely overlap with ROI-based results, except that more significant voxels were detected in the ROI analysis, for instance, in the vmPFC ROI (rACC and paracingulate gyrus). **(B)** Negative-value coding: activations for prospective losses ($\beta_{loss,\,neutral} > 0$) and deactivations for prospective gains ($\beta_{gain,\,neutral} < 0$) in the vmPFC/mOFC; deactivations for prospective gains in the posterior insula and activations for prospective losses in the left amygdala (ROI analysis; small-volume FDR-corrected with $P < 0.05$ and spatial extent threshold of $k \geq 10$ voxels).
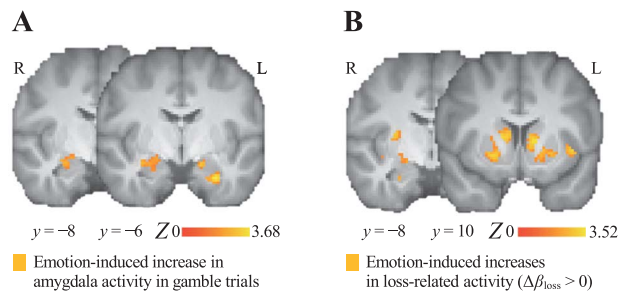
'neural loss aversion' in the right amygdala across subjects (Figure 4D). While activation in this cluster was on average not significantly associated with the size of a prospective gain or loss—that is, both $\beta_{gain,\,neutral}$ and $\beta_{loss,\,neutral}$ were not significantly different from 0 (Figure 4E)—we do observe that the between-subject variability in 'neural loss aversion' can be explained by a negative correlation between loss aversion and activations for prospective losses in this region across subjects (Figure 4F). Since mean activations for prospective gains or losses were not significantly different from zero, this correlation suggests that the most loss-averse participants displayed deactivations (i.e. $\beta_{loss,\,neutral} < 0$) for prospective losses. To investigate this possibility, we extracted parameter estimates for the top quartile of $\lambda_{neutral}$ values (i.e. the most strongly loss-averse individuals). We indeed observed deactivations for losses that were significantly different from 0 ($\beta_{loss,\,neutral} = -2.32$, SD = 2.00), $t(6) = -3.065$, $P = 0.022$. Hence, greater loss aversion was associated with a tendency toward greater deactivations for prospective losses.

Furthermore, we also observed two small clusters in the posterior insula and vmPFC that displayed a positive association between loss aversion and loss-related activations (i.e. negative-value coding, see Supplementary Table S1), consistent with an earlier report of such an association in the posterior insula (Canessa *et al.*, 2013).
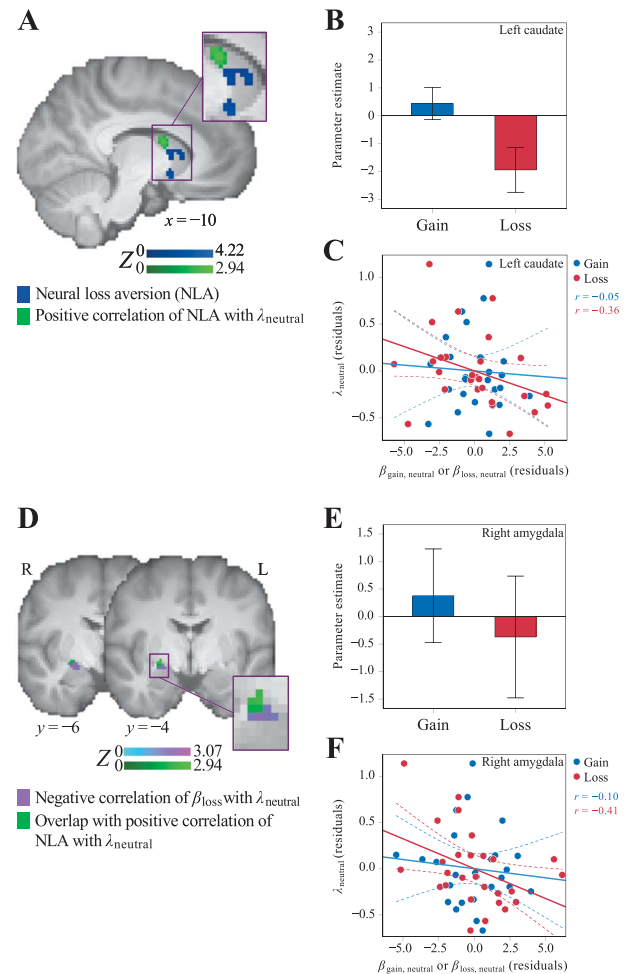
Fig. 4. Neural loss aversion in the neutral-face condition. **(A)** Neural loss aversion, i.e. greater deactivations for losses relative to activations for gains ($-\beta_{loss,\,neutral} - \beta_{gain,\,neutral} > 0$) in the striatum (blue). Neural loss aversion was also positively correlated with individual differences in behavioral loss aversion across participants, e.g. in the left caudate (green). **(B)** Parameter estimates for the gain and loss regressors for the left caudate cluster that displayed neural loss aversion. **(C)** Relationships between neural gain and loss responses and behavioral loss aversion in the left caudate [green cluster in (A)]. Greater deactivations for losses significantly predicted greater loss aversion, $\lambda_{neutral}$ (partial regression plot, i.e. the individually estimated degrees of loss aversion, $\lambda_{neutral}$, are regressed on the second behavioral covariate $\sigma_{neutral}$ that entered the fMRI group-level analysis; the residuals on the vertical axis thus signify the idiosyncratic component of the degree of loss aversion that cannot be explained by decision noise; the same holds analogously for the neural response depicted on the horizontal axis; for a simple regression plot without controlling for decision noise, see Supplementary Figure S1A, left panel). **(D)** Neural loss aversion was positively correlated with behavioral loss aversion in the right amygdala (green), which could be attributed to stronger deactivations for losses with increasing behavioral loss aversion (purple). **(E)** Parameter estimates for the gain and loss regressors for the green amygdala cluster. **(F)** Relationships between neural gain and loss responses and behavioral loss aversion in the amygdala cluster. Greater deactivations for losses significantly predicted greater loss aversion (partial regression plot; for a simple regression plot, see Supplementary Figure S1B, left panel). All statistical tests were small-volume FDR-corrected with $P < 0.05$ and $k \geq 10$. Error bars/lines represent 95% CIs (including between-subject variance).

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

A

R   L

$y = -8$ $y = -6$ Z ▮0 ▮▮▮ 3.68

▮ Emotion-induced increase in amygdala activity in gamble trials

B

R   L

$y = -8$ $y = 10$ Z ▮0 ▮▮▮ 3.52

▮ Emotion-induced increases in loss-related activity ($\Delta\beta_{loss} > 0$)

Fig. 5. Fear-induced changes in gamble- and loss-related activity. (**A**) Increased bilateral amygdala activity following the presentation of fearful faces compared to neutral faces (red–yellow; onset: face presentation, including gamble presentation). (**B**) Fear-induced increases in loss-related activity (i.e. $\beta_{loss,\,fearful} - \beta_{loss,\,neutral} > 0$). All statistical tests were small-volume FDR-corrected with $P < 0.05$ and $k \geq 10$.

Fear-induced changes in neural value responses

In the previous section, we described how loss aversion in the neutral-face condition was associated with asymmetric positive-value coding with greater deactivations for prospective losses relative to activations for prospective gains (i.e. neural loss aversion). We now turn to our hypothesis regarding a shift toward negative-value coding in the fearful-face condition. Specifically, we expected that greater neural activations for prospective losses would mediate fear-induced increases in loss aversion. Furthermore, we hypothesized that this behavioral shift is mediated by amygdala reactivity to incidental fear cues, which spills over to the processing of prospective monetary payoffs.

In line with this hypothesis, we observed a general increase in bilateral amygdala activity during the combined period of face and gamble presentation for fearful faces compared to neutral faces ($\beta_{gamble,\,fearful} - \beta_{gamble,\,neutral} > 0$, see Figure 5A and Supplementary Table S3). We also observed this effect during the gamble presentation when running a model with separate regressors for the presentation of the face stimuli and display of the gambles. For affective priming to work, these two stages of a trial have to be so close in time to each other such that they cannot be clearly separated in fMRI data analysis, given the sluggish hemodynamic response. The two stages were thus modeled as one event in our main analysis. This increase in amygdala activity, however, was not correlated with fear-induced changes in loss aversion across subjects.

The most pronounced manifestation of a shift toward negative-value coding would be a complete *reversal* from positive-value coding to negative-value coding. In terms of loss-related parameter estimates, this would mean that for one and the same voxel, one would observe that $\beta_{loss,\,neutral}$ is significantly smaller than zero *and* that $\beta_{loss,\,fearful}$ is significantly greater than zero. In other words, this criterion amounts to calculating the conjunction of $\beta_{loss,\,neutral} < 0$ and $\beta_{loss,\,fearful} > 0$. This is, however, a very restrictive criterion. And indeed, performing this conjunction analysis does not yield a single cluster whose size exceeds a cluster extent threshold as liberal as $k \geq 2$.

Given that this criterion may be overly strict, we conduct an analysis that is based on the less restrictive criterion $\beta_{loss,\,fearful} - \beta_{loss,\,neutral} > 0$ to detect a shift toward negative-value coding for losses. We found a distributed set of brain regions displaying activations for prospective losses that were significantly greater in the fearful-face condition compared to the neutral-face condition (see Figure 5B and Supplementary Table S3). This

result could be driven by either (i) increased activations for losses (increased negative-value coding) in the fearful-face condition relative to the neutral-face condition, or (ii) reduced or absent deactivations for losses (reduced positive-value coding) in the fearful-face condition relative to the neutral-face condition. To differentiate between these possibilities, we conducted conjunction analyses.

To examine the first possibility, we calculated a conjunction analysis with the thresholded maps for the contrast $\beta_{loss,\,fearful} - \beta_{loss,\,neutral} > 0$ and for $\beta_{loss,\,fearful} > 0$ with a spatial extent threshold of $k \geq 5$ voxels (Supplementary Table S3). Explained verbally, this conjunction reveals clusters in which we observed significant activations to prospective losses in the fearful-face condition that were larger than in the neutral-face condition, indicating increased negative-value coding. One central finding is that this conjunction analysis reveals significant clusters of voxels that fulfill these two criteria in the bilateral amygdala (Figure 6A and B), putamen and mid-anterior insula. It turns out that these regions did not display significant activations to prospective losses in the neutral-face condition (i.e. in the contrast $\beta_{loss,\,neutral} > 0$). Crucially, we also observed that greater fear-induced activations for losses (i.e. $\beta_{loss,\,fearful} - \beta_{loss,\,neutral} > 0$) predicted fear-induced increases in behavioral loss aversion across subjects in the right amygdala (Figure 6A, overlapping with the general increase in loss-related activations, and Figure 6C), vmPFC (Supplementary Figure S2), putamen and insula (Supplementary Table S3). To note, the amygdala cluster is directly adjacent to (and minimally overlaps with) a cluster that displayed the opposite effect in the neutral-face condition—a positive association between deactivations for losses and behavioral loss aversion (see Figure 4D and F). Hence, we observed that loss aversion showed a context-dependent correlation with distinct valuation processes: while baseline loss aversion (i.e. in the neutral-face condition) was positively associated with *deactivations* for prospective losses, fear-induced changes in loss aversion were positively associated with *activations* for prospective losses.

Next, we investigated the possibility that observed activations in our contrast $\beta_{loss,\,fearful} - \beta_{loss,\,neutral} > 0$ reflect reduced or absent positive-value coding in the fearful-face condition relative to the neutral-face condition. This was examined via a conjunction of the thresholded maps for the contrasts $\beta_{loss,\,fearful} - \beta_{loss,\,neutral} > 0$ and $\beta_{loss,\,neutral} < 0$, with $k \geq 5$ (Supplementary Table S3). Several regions that displayed deactivations for losses in the neutral-face condition, including the bilateral striatum (Figure 7A and B), paracingulate gyrus/vmPFC and anterior insula, displayed reduced deactivations for losses in the fearful-face condition but no significant activations for losses. This effect also translated into decreased 'neural loss aversion' in these regions, because by the very definition of 'neural loss aversion,' the strength of deactivations for losses strongly contributes to this feature—see the contrast $(-\beta_{loss,\,fearful} - \beta_{gain,\,fearful}) - (-\beta_{loss,\,neutral} - \beta_{gain,\,neutral}) < 0$ (Supplementary Table S3). Reductions in neural loss aversion were also associated with fear-induced increases in behavioral loss aversion, for instance, in the left caudate (Figure 7A and C and Supplementary Table S3). Even at a very liberal threshold (uncorrected $P < 0.005$ and $k \geq 20$), we did not observe any fear-induced increases in neural loss aversion, or enhanced deactivations for losses in particular, across the whole brain.

Running identical contrasts for prospective gains (i.e. $\beta_{gain,\,fearful} - \beta_{gain,\,neutral}$, and identical conjunction analysis, see Supplementary Table S3), we observed fear-induced deactivations for gains in the fearful-face condition, for instance, in
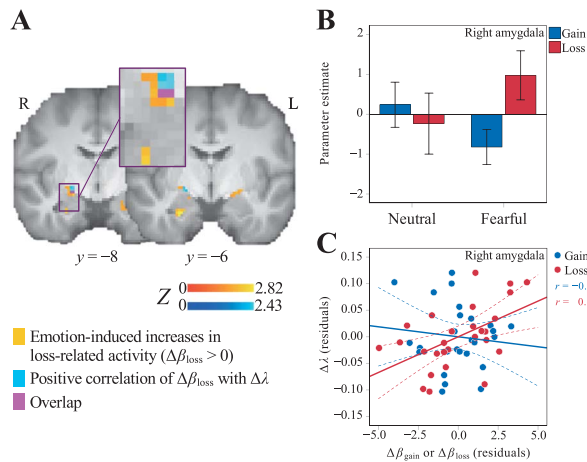
Fig. 6. Fear-induced increases in loss-related amygdala activity. (A) Increased bilateral amygdala activations for prospective losses in the fearful-face condition (red–yellow), which were also associated with fear-induced increases in loss aversion in the right amygdala across subjects (light-blue). (B) Parameter estimates for the gain and loss regressors per condition for the right amygdala [red–yellow cluster in (A)]. (C) Relationships between fear-induced changes in gain and loss responses and changes in behavioral loss aversion in the right amygdala [light-blue cluster in (A)]. Greater fear-induced activations for losses significantly predicted fear-induced increases in loss aversion (partial regression plot, i.e. controlling for $\sigma_{fearful} - \sigma_{neutral}$; for a simple regression plot without controlling for decision noise, see Supplementary Figure S1B, right panel). All statistical tests were small-volume FDR-corrected with $P < 0.05$ and $k \geq 10$. Error bars/lines represent 95% CIs (including between-subject variance).
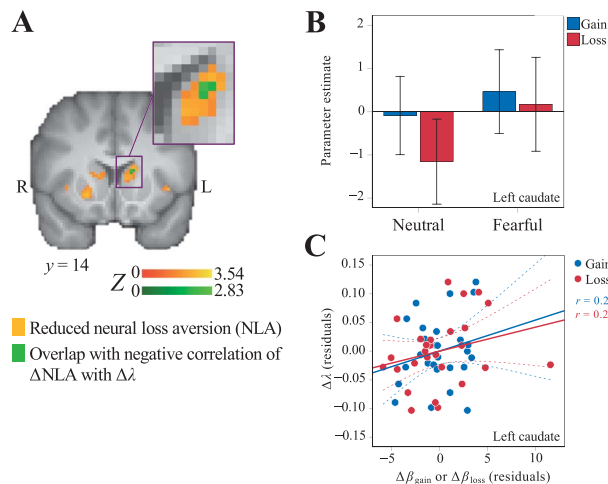
Fig. 7. Fear-induced reduction in neural loss aversion. (A) Reduced neural loss aversion (i.e. $-\beta_{loss} - \beta_{gain}$) in the bilateral striatum in the fearful-face condition compared to the neutral-face condition (red–yellow). Decreases in neural loss aversion were associated with fear-induced increases in behavioral loss aversion in the left caudate (green). (B) Parameter estimates for the gain and loss regressors per condition for the left caudate [red–yellow cluster in (A)]. (C) Relationships between fear-induced changes in gain and loss responses and changes in behavioral loss aversion in the left caudate [green cluster in (A)]. Descriptively, increasing activations for gains and losses were associated with increasing loss aversion, but neither correlation was statistically significant (partial regression plot; for a simple regression plot, see Supplementary Figure S1A, right panel). Their combined effect, however, led to significant reductions in neural loss aversion, which is based on stronger deactivations (and not activations) for losses relative to activations for gains. All statistical tests were small-volume FDR-corrected with $P < 0.05$ ($k \geq 10$). Error bars/lines represent 95% CIs (including between-subject variance).

the right amygdala (Figure 6B) and bilateral putamen. Stronger deactivations for gains in the right amygdala and vmPFC were also associated with fear-induced increases in loss aversion. We also found small clusters in the bilateral putamen and frontal pole that displayed reduced activations for gains relative to the neutral-face condition, but that showed no significant deactivations in the fearful-face condition. Fear-induced increases in loss aversion, however, were associated with greater activations for gains in the right caudate and left posterior insula.

In line with the pronounced fear-induced shifts from positive to negative value coding in several brain regions, an ROI-based conjunction analysis revealed only a partial overlap between neural value responses in the neutral and fearful condition (see Supplementary Table S4). For instance, we observed deactivations for losses in the striatum and anterior insula across conditions, but this pattern was clearly more pronounced in the neutral condition (Supplementary Tables S1 and S2). Furthermore, there was no overlap in a cluster-based whole-brain conjunction analysis, which is also in line with the reported shifts in value coding.

Discussion

The relation between affect and decision making has recently received increasing attention in the psychology (Schulreich *et al.*, 2014; Lerner *et al.*, 2015), economics (Lepori, 2015; Meier, 2019) and neuroscience literature (Phelps *et al.*, 2014; Engelmann *et al.*, 2015; Charpentier *et al.*, 2016). However, the underlying neural mechanisms are currently not well understood. In the present study, we replicated the behavioral finding that incidental fear cues increase monetary loss aversion relative to a baseline with emotionally neutral cues (Schulreich *et al.*, 2016). At the neural level, we found evidence for a context-dependent employment of distinct valuation processes in the two conditions. Specifically, while loss aversion in the neutral-face condition correlated with 'neural loss aversion,' fear-induced increases in loss aversion were associated with increases in negative-value coding. As a result, our study provides a mechanistic explanation of how incidental emotional cues influence decision making.

With the neutral-face condition, we replicated a previously observed feature termed 'neural loss aversion,' that is, greater deactivations for prospective losses relative to activations for prospective gains in a set of regions such as the striatum (Tom *et al.*, 2007; Canessa *et al.*, 2013; Charpentier *et al.*, 2016; Pammi *et al.*, 2017). 'Neural loss aversion,' and loss-related deactivations in particular, also predicted behavioral loss aversion. Notably, we also observed this effect in the amygdala. This is in contrast to the mixed results of some previous studies (Tom *et al.*, 2007; Canessa *et al.*, 2013; Gelskov *et al.*, 2015; Charpentier *et al.*, 2016) but in line with a recent study that found 'neural loss aversion' in the amygdala, though it was unrelated to behavioral loss aversion in that study (Pammi *et al.*, 2017). We also found activations for prospective losses in the left amygdala and in the mOFC/vmPFC, consistent with previous observations (Basten *et al.*, 2010; Canessa *et al.*, 2013; Sokol-Hessner *et al.*, 2013; Häusler *et al.*, 2016). However, in contrast to previous findings (Canessa *et al.*, 2013; Sokol-Hessner *et al.*, 2013), the loss-related amygdala activations that we observed were unrelated to baseline loss aversion. Taken together, while we observed that a few brain areas displayed negative-value coding, a positive-value coding system that exhibits stronger deactivations for losses relative to activations for gains was better able to account for behavioral

loss aversion in a context where no incidental fear cues were present.

With the fearful-face condition, we induced changes in both behavior and brain activation. We observed increased amygdala activity following the presentation of fearful faces relative to neutral faces, in line with meta-analytic findings (Fusar-Poli *et al.,* 2009). Critically, a previous study found that emotion-induced amygdala activity spills over to the subsequent processing of unrelated threat-related stimuli (Pichon *et al.,* 2015). While our research design did not allow for a direct test of a spillover of amygdala activity, given the temporal proximity of the face and gamble stimuli, our findings indicate that the processing of fearful faces altered valuation processes in the amygdala. Specifically, we found that incidental fear cues induced negative-value coding in the amygdala and the putamen—that is, activations for losses as well as deactivations for gains. Furthermore, stronger fear-induced activations for prospective losses in the amygdala, vmPFC and putamen predicted fear-induced increases in loss aversion, which is the exact opposite as in the neutral-face condition. In other words, whereas variations in baseline loss aversion (i.e. in a neutral context) were predicted by 'neural loss aversion,' in particular loss-related deactivations in a set of brain regions, fear-induced increases in loss aversion were predicted by enhanced negative-value coding, in particular loss-related activations. These findings indicate a context-dependent involvement of distinct valuation processes.

This interpretation is corroborated by an exploratory analysis in which we observed that psychopathic personality traits which reflect low fear reactivity attenuated fear-induced increases of loss aversion (see also Schulreich *et al.,* 2016), an effect mediated by attenuated fear-induced increases of loss-related amygdala activations (Supplementary Results S5). At the same time, these traits were unrelated to loss aversion and to deactivations in response to prospective losses in the neutral-face condition. Together, this provides another indication of context-dependent valuation mechanisms.

Remarkably, we did not observe any significant fear-induced increases in loss-related deactivations. This rules out our alternative hypothesis that fear-induced increases in loss aversion were simply due to stronger asymmetric positive-value coding (i.e. increased 'neural loss aversion'). Instead, we observed reduced loss-related deactivations—that is, reduced positive-value coding—in the striatum, anterior insula and rACC/vmPFC. These regions also displayed threat-induced shifts in valuation in a recent study (Engelmann *et al.,* 2015). According to this study, threat of an electric shock negatively impacted the coding of positive subjective expected value in the striatum and the vmPFC. Simultaneously, threat-of-shock induced negative-value coding in the insula, relative to a neutral control condition. Our data indicate that these effects may have been due to loss-related effects—a possibility not explored in the threat-of-shock study because gain and loss responses were not analyzed separately.

Notably, in both our study and the above threat-of-shock study, a reduction in the measured intensity of positive-value coding may have resulted from a compromised coding of losses in the form of deactivations. It may, however, also have resulted from spatially close concurrent activations for losses (i.e. negative-value coding). The latter could have partially or fully canceled out deactivations in a summed fMRI signal. Interestingly, the threat-of-shock manipulation neither induced changes in loss aversion nor changes in amygdala activity. A possible explanation for this absence might be the involvement of different processes, for instance, related to pain: pain-related processes might explain the greater shift toward negative-value

coding in the insula during threat of shock (Engelmann *et al.,* 2015) than after seeing fearful faces because the latter more reliably enhance amygdala activity (Fusar-Poli *et al.,* 2009).

Another study that investigated the influence of fearful (as well as happy) face cues on loss aversion also did not find value-related amygdala activity that predicted emotion-induced increases in loss aversion (Charpentier *et al.,* 2016). In contrast to this, we observed that fear-induced changes in loss-related activations predicted changes in loss aversion. One possible reason for these diverging findings might be the different priming procedures used. While primes with a 3000 ms duration were used in that study, we used primes with a duration of 250 ms (embedded in a gender-identification task), which is within the reported range of 0–300 ms of particularly potent affective priming (Hermans *et al.,* 2001). Another reason might be the moderate sample size and thus statistical power in both their and our study. The study by Charpentier *et al.*, however, found that enhanced amygdalar–striatal connectivity predicted increases in loss aversion following the presentation of fearful and happy compared to neutral faces. This finding complements ours in important ways by suggesting a possible valence-independent emotional component and by supporting the notion that amygdalar inputs to the striatum seem to be critical for avoidance actions (LeDoux and Gorman, 2001).

Our study extends the existing research by linking fear-induced changes in value coding *and* loss aversion to predominantly loss-related effects that we also observed in the amygdala. More generally, our study adds to the growing body of evidence for two opposing neural loss and gain signals that have been related to distinct, but overlapping motivational systems (Brooks and Berns, 2013; Seymour *et al.,* 2015). For instance, consistent with electrophysiological and optogenetic evidence in rodents (Shabel and Janak, 2009; Beyeler *et al.,* 2016), we found intermingled *activation*-based and *deactivation*-based loss signals in the human amygdala. In addition to this, we demonstrate a specific contextual variable that modulates the relative contributions of these opposing loss and gain signals: the presence of incidental fear cues.

Before closing, we would like to add that although changes in observed risk aversion in our mixed-gambles task were captured well by changes in loss aversion in our model, future research might benefit from including additional trials like gain-only trials (e.g. De Martino *et al.,* 2010; Sokol-Hessner *et al.,* 2013) and loss-only trials to better disentangle effects specific to loss aversion from other risk-related effects. Due to fMRI time constraints, however, and given the finding of Novemsky and Kahneman (2005) 'that there is no risk aversion beyond loss aversion' (p. 123) for payoffs that only marginally change participant's wealth, we only included mixed-gamble trials in the present study because we deemed those the crucial ones for our research question. Future studies could also make use of continuous measurements of emotional reactivity. Of particular interest would be unobtrusive recordings of electrodermal activity, whereas immediate explicit self-reports of affective states might disrupt affective priming and retrospective reports may not capture (fluctuating) affective experiences during the task well and are potentially influenced by decision processes.

We conclude that the amygdala, in concert with other regions, provides a neural substrate for the interaction of incidental affect and valuation. Our findings indicate that fear-induced increases in loss aversion can be explained by enhanced activations for losses, that is, a shift toward negative-value coding. In contrast, greater loss aversion in a neutral context was associated with stronger deactivations for losses

across subjects. By taking the neural level into account, we go beyond behavioral models of choice that are agnostic to the source of loss aversion. This enables us to provide evidence that loss aversion is mediated by a context-dependent involvement of distinct valuation processes that represent losses in markedly different ways. The presence and context-dependent involvement of different valuation processes could explain why—despite systematic individual differences—risk preferences are characterized by substantial within-subject variation over time (Schildberg-Hörisch, 2018).

Supplementary data

Supplementary Material is available at *SCAN* online.

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Conflict of interest

The authors declare no conflicts of interest.

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