

Hedonic Context Modulates Risky Choices and Reward Responses in Amygdala and Dorsal Striatum

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The hedonic context of the environment can alter an individual's emotional states and consequently their risk taking. Here we reveal the brain mechanisms underlying music-induced unstable risk preferences using functional MRI (fMRI). Subjects listened to self-selected liked or disliked music while they decided to accept or reject risky gambles. Behaviorally loss aversion was lower during liked music than during disliked or no music. At the neural level, reduced loss aversion was associated with a specific pattern of value coding in amygdala and dorsal striatum: during disliked music gambles with high expected reward induced higher activation than gambles with low expected reward, whereas during liked music this activation pattern was reversed. Furthermore, individual differences in loss aversion influenced value coding in such a way that for the most loss-averse subjects, bilateral activation of anterior insula, dorsolateral prefrontal cortex, and posterior parietal cortex increased as the expected value of the gamble increased, whereas for the least loss-averse subjects increase in potential reward was associated with decreasing activation in those areas. We propose music-modulated value coding in amygdala and striatum as a neural mechanism supporting emotion-dependent adjustments to risk-taking which in turn facilitate behavior depending on how dangerous versus safe the environment is experienced to be.

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Contrary to the standard premise of economic theory, risk preferences are not stable across contexts (Barseghyan et al., 2011; Einav et al., 2012). For example, when returning from an exciting party by a cab late in the night, riding without a seatbelt may not feel risky at all, whereas only a few of us would drive our children to school on Monday morning without fastening their seat belts. In the dynamic preferences model of Laibson (2001), environmental cues and consumption can act as complements: playing French music in a wine shop may increase the marginal utility from consuming French wines for some individuals. It has also been proposed that different types of visceral cues such as drive states, emotions, and subjective feelings may modulate preferences (Loewenstein, 1996, 2000). In addition to modulating preferences for consumption items, similar processes, or preference interactions, could also influence risk preferences.

At the neural level, risk preferences are computed in a network encoding hedonic stimulus value and the associated visceral responses (Platt & Huettel, 2008; Mohr et al., 2010). Amygdala processes emotional valence of external and particularly aversive stimuli (for a review, see Zald, 2003), but also subjective stimulus value (see Seymour & Dolan, 2008). Recent single-cell recordings have also revealed a specific set of amygdalar neurons that encode stimulus value at the time of choice (Jenison et al., 2011). Furthermore, patients with focal bilateral amygdalar lesions show lower sensitivity to financial losses than healthy controls, suggesting that financial risk preferences are computed at least partially in the amygdala (de Martino et al., 2010).

Insula processes somatic information underlying subjective feelings (for a review, see Critchley, 2005), in particular negative emotions such as sadness or anxiety (see Phan et al., 2002 and Vytal & Hamann, 2010 for meta-analysis), and, in decision-making, risk and risk prediction error (Preuschoff et al., 2006; for a review, see Bossaerts, 2010). A recent meta-analysis concluded that risk processing is modulated by potential losses and the modulation is associated with activation in anterior insula (Mohr et al., 2010).

The striatum in turn shows reward-related responses that vary with hedonic environment: In dorsal striatum neural sensitivity to reward

and punishment is abolished under acute stress (Porcelli et al., 2012). In ventral striatum, nucleus accumbens is activated when subjects' decisions shift toward higher risk in trials with positively valenced predecision cues (Knutson et al., 2008).

Here we show that risky choices and neural coding of risk preferences are modulated by short-term changes in the hedonic context of the environment. We have previously shown that listening to liked music increases risk-taking and reduces loss-aversion, whereas disliked music has the opposite effect, relative to the baseline of no music (Halko & Kaustia, 2012). Here subjects played risky gambles involving real monetary gains and losses during fMRI, and were instructed to decide whether or not to participate in each gamble. While performing the gambling task, they listened to self-selected liked or disliked music or no music at all. We used music for mood manipulation because it is a powerful environmental factor and ubiquitous in everyday life, and because music can be used for mood induction without participants paying conscious attention to the mood-inducing stimulus, thus mimicking real-life conditions where environmental factors modulating individuals' emotional states are not constantly attended. We predicted that listening to the liked versus disliked music would increase acceptance of risky gambles, which would be reflected in altered value coding in amygdala, insula and/or striatum.

Method

Participants

The Ethics Committee of the Helsinki and Uusimaa Hospital District approved the study protocol, and the study was conducted in accordance with the Declaration of Helsinki. Altogether 22 healthy subjects participated in the experiment (8 females, mean age 32 years, range 22–50 years; 17 of 22 right-handed). None of the subjects was a professional musician. All subjects were compensated for their travel cost and they signed informed-consent forms.

Behavioral Measures and Music Selection

The experiment consisted of two separate sessions. For the first session subjects were

asked to select and bring with them four pieces of music they liked and four pieces of music they disliked on CDs or MP3 files. The subjects filled out questionnaires on reward drive (The BIS/BAS questionnaire, Carver & White, 1994), emotional contagion (Emotional Contagion Scale, Hatfield et al., 1994), risk attitudes (Dohmen et al., 2011; Halko et al., 2012), and socioeconomic and music background. In the music background questionnaire, we also asked the subjects why they liked or disliked the music tracks they selected. The date and the time of the second session were scheduled, leaving at least one week between the sessions. A fixed payment of 20 euros was paid and the subjects were reminded that in the subsequent fMRI experiment they could either win or lose money.

Each individual's liked and disliked music was converted to MP3 format and processed using Audacity software (<http://audacity.sourceforge.net>): To reduce amplitude differences within each piece of music the eight pieces underwent dynamic range compression, and peak amplitudes were normalized across pieces. Finally, a 2-min section of each music piece was chosen for the subsequent (fMRI) session.

Upon arriving for the fMRI session, it was explained to the subjects that their task was to accept or reject gambles that offered a 50–50 chance to win or lose money (de Martino et al., 2010; Tom et al., 2007). Because we were interested in the brain activation at the moment of decision-making, and because prior earnings influence risk-taking (Coval & Shumway, 2005; Gneezy et al., 2003; Thaler & Johnson, 1990; Weber & Zuchel, 2005), the subjects were not shown the outcomes of their chosen gamble after each trial. They were told that at the end of the experiment two gambles would be randomly drawn, and the ones that the subject had accepted would be played for real money. We adopted the two-session structure to make the subjects feel that they would face actual potential losses in the gambles, and less likely to feel as if they were “gambling with the house money” (Rosenboim & Shavit, 2012; Tom et al., 2007). The total payment for each participant included a 20 euro fixed fee (first session) and earnings from two randomly chosen gambles (second session).

Before entering the MRI scanner, the participants rated valence (from 1 = *unpleasant* to

10 = *pleasant*) and arousal (from 1 = *calm* to 10 = *aroused*) of their four liked and four disliked music pieces on a visual analog scale, and practiced the decision-making task both with music on and music off.

Behavioral Task

During fMRI participants underwent two imaging runs of 22 min each. Both runs comprised 8 blocks of the gambling task: 4 blocks while listening to either liked or disliked music and 4 blocks without music. Each block consisted of 16 gamble trials (Figure 1A). Within each trial, the gamble was presented for 2500 ms on a gray background, followed by a blank gray screen until the onset of the next gamble. Subjects had 2.5 seconds to either accept or reject the gamble by button-press. The response times were measured from the time the gamble was presented until the response was made by the participant.

There were 16 different gain outcomes ranging from 10 to 40 euro, and 16 loss outcomes ranging from 5 to 20 euro. Each subject went through the full payoff matrix of $16 \times 16 = 256$ gambles; all gambles were presented once, and none of the gambles were repeated. To ensure an even mix of different types of gambles under all three conditions, we defined 16 separate areas within the payoff matrix, each comprising 4×4 gambles. The 16 gambles per block were then obtained through random sampling of one gamble from each of the 16 areas (Figure 1B). Music manipulation and behavioral task were chosen to be very similar to an earlier study, conducted with a different group of subjects (Halko & Kaustia, 2012).

To separate neural responses to music (in blocks) from responses to gambles (in trials within blocks), the experiment used a mixed block/event-related design (Chawla et al., 1999; Petersen & Dubis, 2012). To enable simultaneous modeling of music-versus gamble-related brain activity, we minimized the correlation between the respective predictors in fMRI analysis through trial timing as in Chawla et al. (1999): each set of 16 within-block trials contained one long stimulus onset asynchrony (SOA, gamble onset to gamble onset) of up to 24.2 s ($12 \times \text{TR}$ of 2.016 s). The position of the long SOA within the block of 16 trials was counterbalanced across conditions. In all blocks, the minimal SOA was 4.0 s ($2 \times \text{TR}$). As our main aim was

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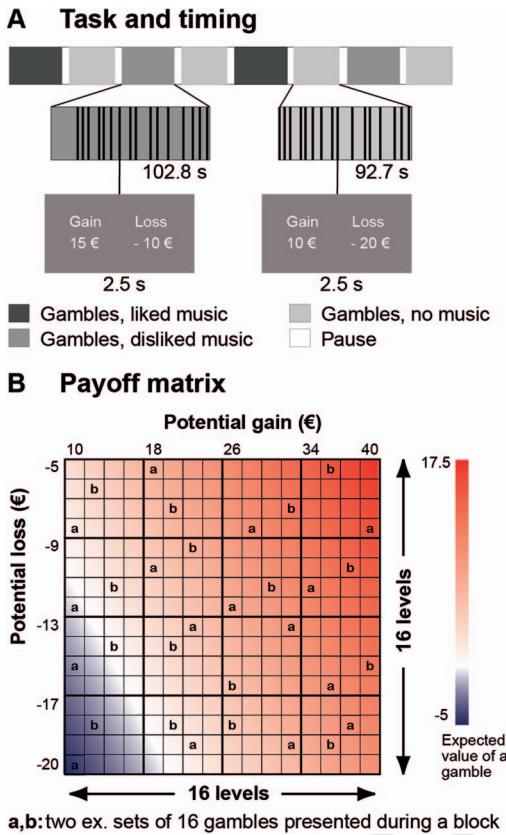


Figure 1. The financial decision-making task. (A) The task of the subjects was to accept or reject gambles that offered a 50–50 chance of gaining or losing money. Within each of the two fMRI imaging runs, subjects played eight different blocks of 16 gambles. Each block corresponded to either liked music, disliked music, or no music. A block with music was always followed by a block without music. A block with music started with 10.1 s (corresponding to $5 \times \text{TR}$) of music only, followed by 92.7 s ($46 \times \text{TR}$) of music and gambles. Sixteen gambles were presented on screen with a stimulus onset asynchrony (SOA) of minimally 4.0 s ($2 \times \text{TR}$) and maximally 24.2 s ($12 \times \text{TR}$). There was a 16.1-s ($8 \times \text{TR}$) pause between the blocks. In each of the two imaging runs, the total duration of the decision making task was approximately fifteen min. (B) The payoff matrix comprised 256 different gambles. Gains ranged from 10 to 40 euro, in increments of 2 euro, and losses from 5 to 20 euro, in increments of 1 euro. The 256 gambles were divided into 16 sets of 16 gambles each. Within a set, the 16 gambles were scattered around the payoff matrix such that only one gamble came from each of the separate 4×4 areas in the matrix. In the figure, the letters a and b represent two examples of a set of 16 gambles, one set presented per block. The blue–red color scale depicts the expected value (EV) of a gamble: $\text{EV} = 0.5 \times \text{gain} + 0.5 \times \text{loss}$.

to study trial-wise responses to gambles, rather than block-wise responses to music, music blocks were 102.8 s long ($51 \times \text{TR}$), for two reasons: blocks had to be (a) long enough for mood induction to become effective, and (b) long enough to allow presentation of 16 gambles per block, one from each of the 16 areas of the payoff matrix (Figure 1A and 1B).

Across subjects, two counterbalanced orders of the Liked music (L) and Disliked music (D) were used and a block of music was always followed by a block of gambles without music (N). The possible counterbalancings were LNDNLNDN–LNDNLNDN and DNLNDNLN–DNLNDNLN. To analyze the neural responses to music in the absence of decision making task, the four pieces of music per imaging run were replayed after the decision making task ($4 \times 50 \text{ TR}$).

Behavioral data collected were used to quantify behavioral loss aversion for each participant (Kahneman & Tversky, 1979). The loss aversion parameter expresses how much more sensitive subjects are to losses than gains, and was estimated by fitting a logistic regression to each participant’s acceptance decisions, using the size of the win and loss as independent variables without a constant in the model. The loss aversion parameter was calculated as the ratio of the logit regression coefficients $\text{beta}(\text{loss})$ and $\text{beta}(\text{win})$. The analysis is based on a common simplifying assumption of a linear value function and identical decision weights (Tom et al., 2007).

MRI Data Acquisition and Analysis

Immediately before fMRI data acquisition, a series of mock scans served to ensure easy audibility of music in the scanner; otherwise we used standard parameters for whole-head fMRI data acquisition and preprocessing (see Supplementary Material). At a single-subject level, the gamble events within blocks of music (see Figure 1) were modeled using two types of regressors, all convolved with canonical hemodynamic response functions: (a) the two types of music were modeled using boxcar functions, with one predictor for two blocks of liked music per run (102.8 s each), one predictor for two disliked music per run (102.8 s each), and with no separate predictor for nonmusic blocks, and (b) individual gamble events within each block

using stick functions, with the size of the expected value of a gamble ($EV = 0.5 \times \text{gain} - 0.5 \times \text{loss}$) as a single parametric modulator. This model will be referred to as parametric EV model. To separate the gambles with same expected value but different standard deviation (*SD*) we added the *SD* of a gamble to the parametric EV model as a second parametric modulator and rerun the analysis. We also studied separately the effects of the size of the gain and the size of the loss. Gamble events were modeled using the same regressors as above, but the EV was replaced with the absolute size of gain and the absolute size of loss of a gamble as separate parametric modulators. This model will be referred to as parametric gain–loss model.

The data analysis involved three approaches: First, we analyzed brain responses to the expected reward, here to the expected value of a gamble, using the parametric EV model, and after, brain responses to the size of the gain and size of the loss of a gamble separately using the parametric gain–loss model. This analysis identified brain regions where activity varied with the EV of gambles and which responded specifically to the size of gain and/or loss. To maximize statistical power, this analysis included all gamble trials, regardless of music condition. To test whether individual differences in loss aversion influence cerebral responses, subject-wise behavioral loss aversion scores were included as a covariate in the random effects (RFX) analysis.

In the second approach, we analyzed interactions between music and value coding using the parametric EV model. Full-volume analyses were complemented with region-of-interest (ROI) analyses in the reward and emotion circuits. The anatomically defined bilateral ROIs included amygdala and dorsal striatum (caudate and putamen), which were defined on the basis of the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002; ROI volumes from <http://sourceforge.net/projects/marsbar/files/>). Two further regions involved in short-term changes in risk taking (Knutson et al., 2008)—bilateral insula as defined on the basis of the AAL atlas, and nucleus accumbens as defined by a 5-mm radius sphere centered at $\pm 12, 9, -8$ (Cauda et al., 2011)—were also included as ROIs. RFX analyses were performed using contrast images for parametric responses to EV during

liked music > parametric responses to EV during disliked music, and vice versa.

To make the parametric response results more accessible, we repeated the previous analysis by dividing the gambles in three groups: high-, medium-, and low-value gambles. To define the groups, the 16 gambles within each block were sorted according to their expected value. Per block, the 5 trials with highest EV were labeled “high-EV,” the 5 trials with lowest EV “low-EV” and the remaining 6 trials “medium EV.” Onset vectors for each category defined 3 predictors that replaced the all-trial onset vector with EV modulation in the parametric EV model, thereby resulting in a categorical EV model. Estimated beta values for the high- and low-EV predictors were then read from the models, averaged across all voxels for the respective ROI, and compared between music conditions.

In the third and last approach, we quantified neural responses to music as such using the music block regressors (see Supplementary Material). This analysis was initially performed with whole-brain search volume, then with anatomically defined bilateral ROIs defined on the basis of earlier studies on emotional perception from music (Koelsch et al., 2006; Mitterschiffthaler et al., 2007).

All models included six realignment parameters as nuisance regressors. Statistical maps were created using thresholds $p < .001$ (uncorrected) at voxel level and $p < .05$ (with family wise error correction) at cluster level. Locations of suprathreshold clusters are reported in MNI coordinates.

Results

Behavioral Results

Choices for liked music pieces were explained with statements like “beautiful melody,” “has a great feel,” “makes me feel good,” and choices for disliked music pieces with statements like “annoying, monotonic melody,” “has a depressing, gray feel,” “tedious and long-winded.” Mean valence was significantly higher and arousal significantly lower when liked rather than disliked music was playing (9.13 vs. 1.59, paired *t* test, two sided, $p < .001$; arousal, 4.20 vs. 6.13, $p < .001$).

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On average, 48.5% of the gambles were accepted (Figure 2A). The acceptance rates were around 50% along the diagonal where the ratio of the win amount to the amount of loss is 2:1, and decreased when moving toward less favorable gambles. Average response times were also the slowest around the diagonal (Figure 2B).

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The frequency for accepting a gamble was 48.5% when no music was played, and it increased to 50.1% when liked music was played and decreased to 46.9% when disliked music was played. Statistical significance and robustness of the result was confirmed by two types of regression models: a linear probability model (OLS) and a logit-model (see Table 1). Compared with no-music and disliked music, liked music increased the likelihood of accepting gambles. The disliked music had no significant effect on gamble acceptance. In all three mod-

els, the coefficient of liked music was significantly larger than the coefficient of disliked music (Wald-tests, $p = .02$, $p = .02$, $p = .04$).

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The behavioral loss aversion parameter (see, e.g., Tom et al., 2007) was calculated as the ratio of the logit regression coefficients beta(loss) and beta(win) and yielded a mean of 2.18 ($SD = 0.79$). The parameter value indicates that in making decisions participants weighted losses approximately twice as much as gains. When the behavioral loss aversion parameter was calculated separately for liked music and disliked music trials, liked music significantly reduced loss aversion (mean 2.06 vs. 2.20, paired t test, two-sided $p = .05$).

Individual differences in both behavioral inhibition (BIS) and emotional contagion (EC) were associated with behavioral measures. Subjects with high BIS scores accepted less gam-

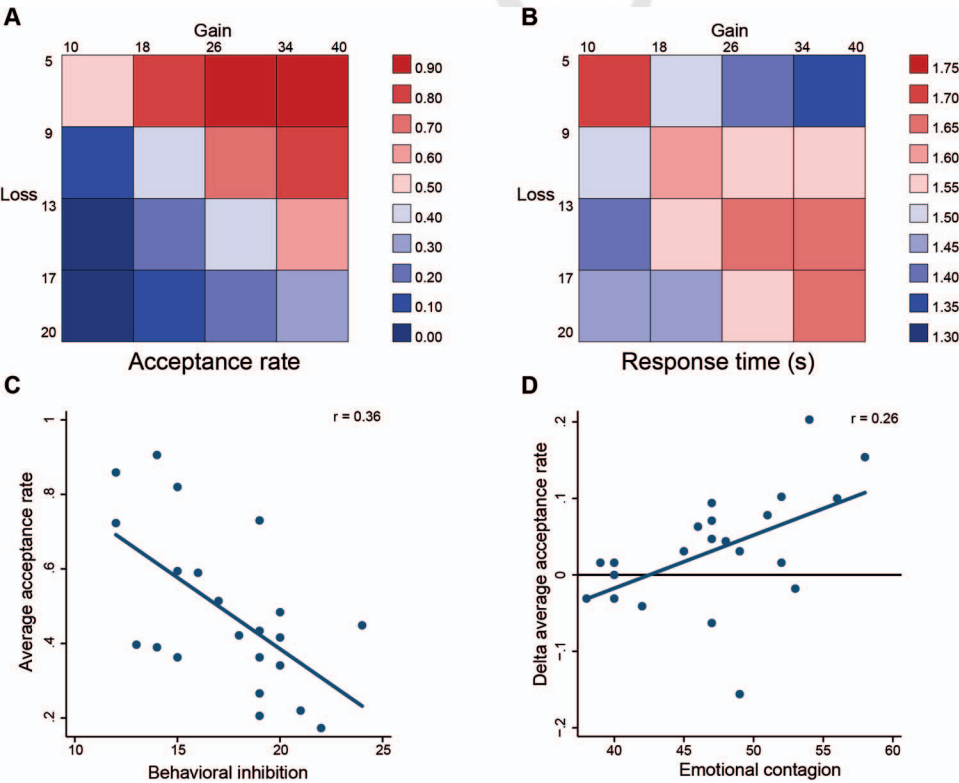


Figure 2. Behavioral results. (A) Payoff matrix and mean acceptance rates, all gambles. (B) Payoff matrix and mean response times (s), all gambles. (C) Scatterplot of correspondence between average gamble acceptance rate and behavioral inhibition scale. (D) Scatterplot of correspondence between delta average acceptance rate = average acc. rate during liked music—average acc. rate during disliked music and emotional contagion.

Table 1
Results From Three Different Regression Models Testing the Effect of the Musical Condition on the Decision to Accept the Gamble

Regression	Liked music	Disliked music
A: Regressions with all subjects		
Linear probability model (OLS)	0.036*** (2.76)	0.004 (0.33)
OLS with subject fixed effects	0.036*** (3.50)	0.004 (0.39)
Logit, subject random effects	0.381*** (3.49)	0.052 (0.41)
B: Subject-specific regressions		
Mean coefficient	0.387*** (2.92)	−0.069 (0.43)

Note. A shows tests of differences in acceptance compared to ‘No music.’ *t* statistics, or *z* statistics for logit regressions, are presented in parentheses below the coefficients. Individual heterogeneity was taken into account adding subjects’ fixed effects into the linear probability model and using subject random effect in the logit-model. In calculating the *t* statistics we use standard errors robust to heteroskedasticity in all analyses, and for fixed effects and random effects models such standard errors are obtained with bootstrapping. B shows results from running separate logit regressions for each subject, and taking averages of the subject-specific coefficients. The *t* statistics in B are from a standard *t* test of means. All regressions included the EV of the gamble as a control variable (not reported). Statistical significance at the 1% level is indicated by.***

bles (Figure 2C, pairwise correlation $r = -0.60$, $p = .003$), were more loss averse ($r = .63$, $p = .002$), and gave slower responses in the gambling task ($r = .51$, $p = .02$) than subjects with low BIS scores. Subjects with high EC scores also accepted less gambles ($r = -0.44$, $p = .04$), were more loss averse ($r = .48$, $p = .02$) and gave slower responses in the gambling task ($r = .50$, $p = .02$), but, in addition, music had a large effect in their behavior. Emotional contagion was associated with the acceptance rates between liked and disliked music (Figure 2D, $r = .51$, $p = .01$), and, correspondingly, with large difference in loss aversion between liked and disliked music ($r = .62$, $p = .004$).

At the end of the experiment two gambles would be randomly drawn, and the ones that the subject had accepted were played for real mon-

ey. The average total payment was 26.23 euros ($SD = 15.75$).

Regional Effects in fMRI

Encoding potential reward. Responses to gamble onset yielded a widespread activation comprising multiple cortical areas, including bilateral insula and bilateral dorsolateral prefrontal cortex, as well as bilateral thalamus (see Supplementary Material, Figure S1), all areas related to the processing of risk in the brain (Mohr et al., 2010). As the EV of a gamble increased, activation increased in left and right inferior occipital cortex and in left superior parietal cortex (see Table 2). As the EV of the gamble increased, activation decreased only in left superior temporal gyrus. The occipito-

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Table 2
Brain Regions With Statistically Significant Parametric Responses to the Expected Value of a Gamble

Activated region	Laterality	Coordinates	Cluster size	$Z_{\max}$	p value
(a) Positive response					
Superior parietal lobule	L	−24 −72 44	703	4.37	$p < .001$
Inferior occipital gyrus	L	−30 −96 −6	1236	4.44	$p < .001$
Inferior occipital gyrus	R	24 −92 0	663	4.19	$p < .001$
(b) Negative response					
Superior temporal gyrus	L	−64 −22 4	242	3.86	$p = .028$

Note. RFX $N = 22$, voxel-level threshold of $p < .001$, cluster-level threshold of $p < .05$, family-wise error correction, whole brain, cluster size in voxels of $2 \times 2 \times 2 \text{ mm}^3$.

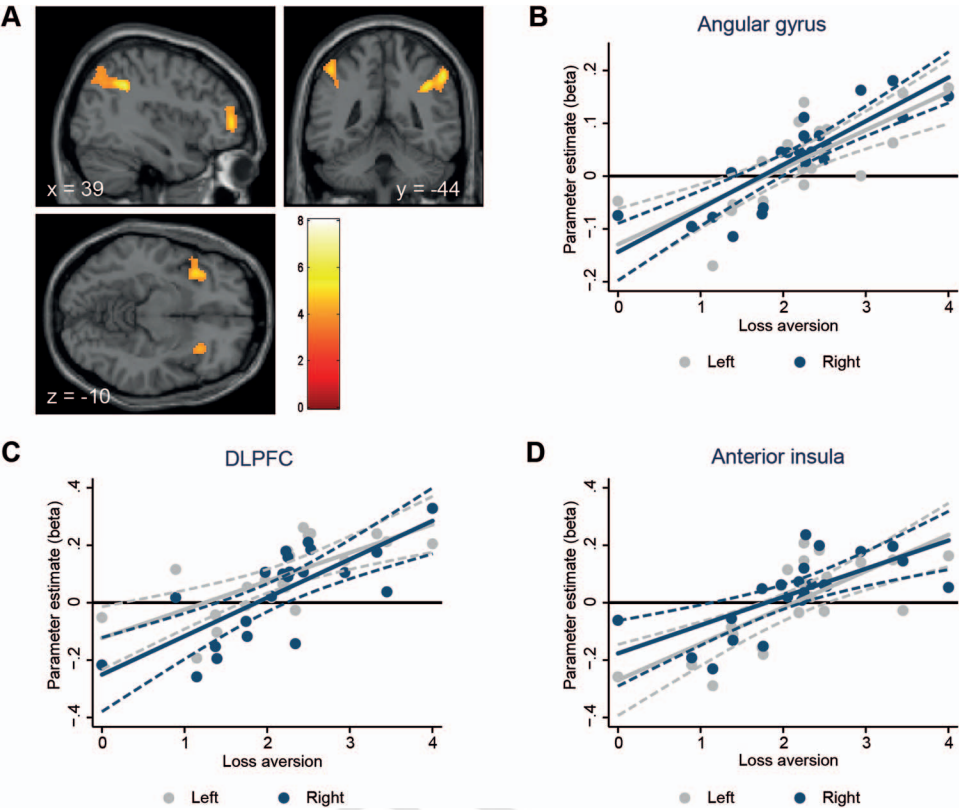


Figure 3. Encoding potential reward. (A) Regions with significant positive correlation between the parametric response to the expected value of a gamble and behavioral loss aversion across participants: bilateral angular gyrus/inferior parietal region (left not shown), bilateral insula, and bilateral middle frontal gyrus. The activation exceeded a voxel-level threshold of $p < .001$ and a cluster-level threshold of $p < .05$, family-wise error correction. (B) Average betas from left and right angular gyrus/inferior parietal region clusters and behavioral loss aversion. Betas calculated from a 6-mm-radius sphere, center at $-42 -36 40$ (left) and at $36 -48 36$ (right). (C) Average betas from left and right middle frontal gyrus clusters and behavioral loss aversion. Betas calculated from a 6-mm-radius sphere, center at $-44 32 24$ (left) and at $38 52 2$ (right). (D) Average betas from left and right insular and inferior frontal clusters and behavioral loss aversion. Betas calculated from a 6-mm-radius sphere, center at $-48 20 -14$ (left) and at $32 22 -10$ (right). The scatterplots (B–D) include regression lines and 95% confidence intervals for visualization only.

parietal activations likely reflect the effects of enhanced attention during the better gambles (Fox et al., 2006; Spreng et al., 2013) co-occurring with cross-modal deactivation in superior temporal auditory areas (cf. Hairston et al., 2008). Adding the standard deviation of a gamble to the model as a second parametric modulator resulted in only negligible changes in the results (Supplementary Table S1).

When parametric responses to the EV were modeled with subject-wise behavioral loss aversion scores (RFX analysis with individual loss

aversion as covariate), a significant positive correlation was observed in the bilateral anterior insula, bilateral angular gyrus (PPC), and bilateral middle frontal gyrus (DLPFC; Figure 3 and Table 3). For the most loss-averse subjects, activation of these areas increased as the EV of the gamble increased, whereas for the least loss-averse subjects, fronto-insular-parietal activation decreased as the EV increased. No negative associations were observed between parametric responses to the EV and behavioral loss aversion. Again the standard deviation of a gamble

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Table 3
Brain Regions With Significant Positive Correlation Between the Parametric Response to the Expected Value of a Gamble and Behavioral Loss Aversion Across Participants

Activated region	Laterality	Coordinates	Cluster size	Z _{max}	p value
Angular gyrus (extending into inferior parietal region)	R	38 -48 36	1032	5.31	p < .001
Inferior parietal region (extending into angular gyrus)	L	-42 -36 40	696	4.12	p < .001
Insula	R	32 22 -10	207	3.58	p = .042
Insula	L	-48 20 -14	425	4.50	p < .001
Middle frontal gyrus	R	38 52 2	220	4.04	p = .034
Middle frontal gyrus	L	-44 32 24	227	3.91	p = .030

Note. Voxel-level threshold of $p < .001$, cluster-level threshold of $p < .05$, family-wise error correction, whole brain, cluster size in voxels of $2 \times 2 \times 2 \text{ mm}^3$.

had only minimal effects on the results (Supplementary Table S2).

Encoding potential losses and gains. Next we analyzed how parametric responses to the size of the gain and to the size of the loss varied with subject-to-subject behavioral loss aversion. Parametric responses to potential gains and behavioral loss aversion showed significant positive correlation in a single cluster in right angular gyrus (see Figure 4). For the most loss-averse subjects the parameter estimate was positive, indicating that an increase in the size of win increased activation in the right angular gyrus. For the least loss-averse subjects an increase in the size of win either did not activate this area or even deactivated it.

Among the areas with EV-related activation (Figure 3A), anterior insula and DLPFC showed significant negative correlation between the parametric response to absolute values of potential losses and behavioral loss aversion across participants (Figure 4, Table 4). In the least loss-averse subjects, activation in those areas increased as the absolute size of losses increased. Conversely, for the most loss-averse subjects, activation decreased as the absolute size of loss increased.

Interactions between music and value coding. When we compared parametric responses to the expected value of a gamble between liked and disliked music trials, no cerebral clusters exceeded thresholds adjusted for whole-brain search volume. With respect to the five predefined ROIs, differences in parametric responses to the EV for liked < disliked music were found in a cluster of 50 voxels ($2 \times 2 \times 2 \text{ mm}^3$) in amygdala ($Z_{\text{max}} = 3.57$, peak voxel $-24 \ 0 \ -18$) and in smaller clusters in putamen and caudate nucleus but neither in insula nor in

nucleus accumbens (see Table 5). None of the ROIs showed parametric responses to the EV for liked > disliked music even with a lenient voxel-level threshold ($p < .005$).

In a follow-up analysis we compared responses to the high-EV versus low-EV gambles while listening to liked versus disliked music. This categorical analysis was based on a model with separate predictors for onset of high-EV, medium-EV and low-EV trials. For each of the ROIs with suprathreshold voxels in the parametric analysis (amygdala, putamen, and caudate nucleus), responses were smaller for low versus high EV during disliked music, with a reverse response profile during liked music. This music type $\times$ level of EV interaction was studied through region-by-region ANOVA. After correction for multiple comparison across the 5 predefined ROIs, the interaction was significant in bilateral amygdala ($p = .04$) and in bilateral putamen ($p = .01$; Figure 5; see legend for ANOVA results). Results from parametric and categorical analysis of amygdala and striatal activation thus converge on music-condition-related differences in value coding.

Activation elicited by liked versus disliked music. Finally, we quantified activation to liked and disliked music as such, based on the music-only blocks. Auditory cortex activation was found in the disliked > liked contrast (see Supplementary Material).

Discussion

For the first time, we show how cerebral expected reward coding is influenced by the hedonic tone of the environment, here induced indirectly by means of music. We confirm the earlier finding that subjectively preferred music

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F5

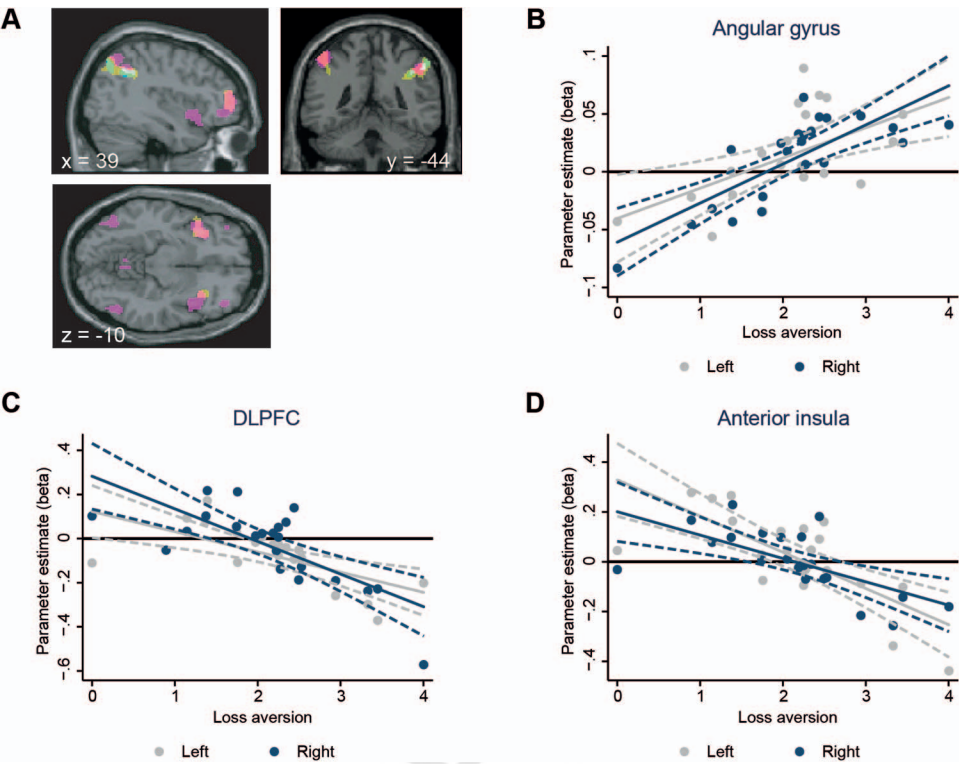


Figure 4. Encoding potential losses and gains. (A) Magenta: Regions with significant negative correlation between parametric response to the absolute size of the loss and behavioral loss aversion across participants, namely bilateral anterior insula and bilateral middle frontal gyrus (right not shown; see Table 4 for full list of areas). Cyan: Region with significant positive correlation between parametric response to the size of the gain and behavioral loss aversion across participants, namely angular gyrus. Yellow: Regions with significant negative correlation between parametric response to the expected value and behavioral loss aversion across participants (same clusters as in Figure 3A), shown for comparison with magenta and cyan clusters. Across all clusters, voxel-level threshold of $p < .001$ and cluster-level threshold of $p < .05$, family-wise error correction. (B) Average betas from left and right angular gyrus/inferior parietal region clusters and behavioral loss aversion. Betas calculated from a 6-mm-radius sphere, center at $-42 -36 40$ (left) and at $36 -48 36$ (right). (C) Average betas from left and right middle frontal gyrus clusters and behavioral loss aversion. Betas calculated from a 6-mm-radius sphere, center at $-44 32 24$ (left) and at $38 52 2$ (right). (D) Average betas from left and right insular and inferior frontal clusters and behavioral loss aversion. Betas calculated from a 6-mm-radius sphere, center at $-48 20 -14$ (left) and at $32 22 -10$ (right). The scatterplots (B–D) include regression lines and 95% confidence intervals for visualization only. Coordinates in B through D chosen to match Figure 3 (B–D).

increases financial risk-taking and reduces loss aversion: compared with the earlier behavioral study with same stimulus and same music manipulation, regression coefficients related with liked music condition were very similar (Halko & Kaustia, 2012). At the neural level, short-term changes in loss aversion were associated with robustly distinct

pattern of value coding in amygdala and dorsal striatum: during disliked music gambles with high expected reward induced higher activation than gambles with low expected reward, whereas during liked music this activation pattern was reversed. As amygdala and dorsal striatum are known to be involved in emotion- and reward-related processing, our result sug-

Table 4
Brain Regions With Significant Negative Correlation Between The Parametric Response To Potential Losses and Behavioral Loss Aversion Across Participants

Activated region	Laterality	Coordinates	Cluster size	Z _{max}	p value
Middle frontal gyrus	L	−38 48 16	995	4.80	p < .001
Cerebellum (extending into left inferior occipital and left inferior temporal lobes)	L	−2 −82 −28	848	4.42	p < .001
Cerebellum	R	2 −60 −18	406	4.35	p = .003
Middle cingulate	L & R	−2 −28 28	227	4.35	p = .04
Middle frontal gyrus	R	44 52 6	432	4.34	p = .002
Inferior frontal gyrus (extending into insula and temporal pole)	L	−38 16 −14	720	4.33	p < .001
Inferior parietal cortex	L	−32 −60 60	1357	4.12	p < .001
Inferior parietal cortex	R	38 −64 54	1090	4.12	p < .001
Cerebellum	L	−26 −64 −40	376	4.06	p = .005
Insula (extending into inferior frontal gyrus and temporal pole)	R	42 10 −8	461	4.00	p = .002
Superior medial frontal cortex (extending into supplementary motor area)	L & R	−2 30 40	481	3.92	p = .001
Precuneus	L & R	−4 −68 50	361	3.81	p = .011

Note. Voxel-level threshold of $p < .001$, cluster-level threshold of $p < .05$, family-wise error, whole brain, cluster size in voxels of $2 \times 2 \times 2 \text{ mm}^3$.

gests that music-induced emotions can influence neural encoding of value, thereby supporting preference interaction on a short time scale and behavioral changes in loss aversion.

In addition to short-term mood states, individual differences in loss aversion also influenced neural encoding of risky choices. For loss-averse subjects increase in potential reward was associated with stronger activation and for non-loss-averse subjects with weaker activation in anterior insula, DLPFC, and PPC, all associated with neural processing of risk.

Table 5
Regions of Smaller Parametric Responses to the Expected Value During Liked Music as Compared With Disliked Music

ROI (all bilateral)	Coordinates	Z _{max}	Cluster size	p value
Amygdala				
Left	−24 0 −18	3.57	50	p = .005
Putamen				
Left	−28 6 −2	3.17	4	
Right	22 2 −2	3.31	2	
Caudate nucleus				
Left	−4 10 4	3.46	6	p = .092
Right	22 22 4	3.24	1	

Note. No suprathreshold activation in insula nor in nucleus accumbens. Voxel-level threshold $p < .001$, voxel counts refer to $2 \times 2 \times 2 \text{ mm}^3$ voxels. Cluster-level p values reported if $< .10$.

Music-Induced Emotional Context Modulates Value Coding in the Amygdala and Dorsal Striatum

Previous studies have shown that amygdala is critical for encoding loss aversion: Unlike healthy controls, patients with bilateral focal lesions in amygdala do not show behavioral loss aversion (de Martino et al., 2010). Moreover, a study using voxel-based morphometry found positive correlation between left-amygdalar gray matter volume and behavioral loss aversion (Canessa et al., 2013). In addition, when subjects choose between a mixed gamble and a sure option, trying to regulate one’s emotions reduces loss aversion as well as amygdala responses to losses (Sokol-Hessner et al., 2009, 2013). Modulation of value coding during liked versus disliked music could also result from integrating stimulus values in the amygdala. For example, the valence (pleasantness) of olfactory stimuli affects how amygdala responds to changes in intensity of the same stimuli (Winston et al., 2005). Altogether our results support the notion that amygdalar response profiles are associated with behavioral loss aversion, and suggest that environmental cues of emotions are integrated with the valuation of choice options in amygdala.

Because most of the low-EV trials were rejected and high-EV trials accepted, in-

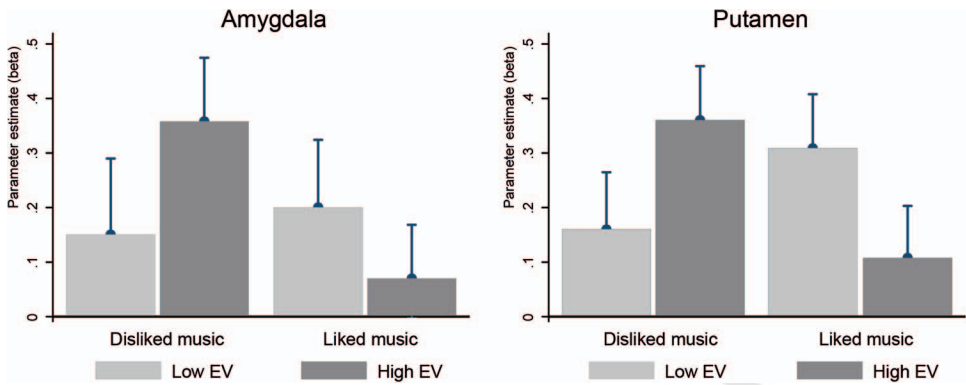


Figure 5. Music and value coding. (A) Beta-values averaged across all voxels in left and right amygdala (bilateral ROI) for music type $\times$ level of the expected value (EV). ANOVA, significant interaction, $F(1, 21) = 8.468$, $p = .008$, after correction for multiple comparison across 5 predefined ROIs, $p = .04$. (B) Beta-values averaged across all voxels in left and right putamen for music type $\times$ level of EV. ANOVA, significant interaction, $F(1, 21) = 12.822$, $p = .002$, after correction for multiple comparison across 5 predefined ROIs $p = .01$. Error bars indicate the standard error of mean (SEM). See the online article for the color version of this figure.

creased amygdala activation was associated with two distinct types of behavior: rejecting low-EV trials while liked music was playing and accepting high-EV trials while disliked music was playing. Amygdala activation thus does not only reflect the choices an individual makes, but also to the environment in which choices were made. This accords with prior work showing that amygdala activation during decision making is contingent on decision-frame-dependent behavior: Amygdala activation increases both during choosing a safe option in the positive ‘gain’ frame and choosing a risky option in the negative ‘loss’ frame, in respect to the opposite behavior (de Martino et al., 2006). In the present study, the participants thus might have interpreted the background music, or pleasantness/unpleasantness of the environment, as the decision frame, which automatically influenced the expected reward coding in amygdala.

We also observed music-related modulation of value coding in dorsal striatum (putamen). When participants made decisions while disliked music was playing, high-EV gambles elicited significantly higher activation than low-EV gambles in putamen. When decisions were made while liked music was playing, a reverse response profile was observed. Dorsal striatum differs from other re-

ward-processing areas in that it encodes an integrated measure of subjective value, combining reward magnitude with further information relevant to the decision task, for example, the delay of reward delivery (Pine et al., 2009). In our experiment, music pieces may have affected the dorsal-striatal value encoding through a similar integration process, thereby supporting the music-related changes in loss aversion. Such neural integration could support preference interaction between music and risk preferences: a person might evaluate a risky gamble higher while listening to their favorite music (Halko & Kaustia, 2012; Laibson, 2001; Loewenstein, 1996, 2000). Especially the low-EV gambles elicited higher activation in putamen when decisions were made while liked music was playing. The higher evaluation may be attributable to a change in how a person evaluates the gain and loss payoffs and/or how she weights the probabilities. A study with a dual lottery task where subjects chose the riskier lottery more frequently after happy (vs. sad or neutral) music, suggests a music-induced change especially in probability weighting (Schulreich et al., 2014). In our study, the gain and loss payoffs varied but the probabilities were held fixed that makes such music-

induced changes in probability weighting less likely.

Individual Differences in Decision-Making Processes

In bilateral anterior insula, DLPFC, and PPC (angular gyrus), parametric responses to the value of gambles varied as a function of subjects' loss aversion. For the most loss-averse subjects, activation increased as the expected value of the gamble increased, and vice versa for the least loss-averse subjects.

All three regions, anterior insula, DLPFC, and PPC, support decision-making under uncertainty (for a review, see [Platt & Huettel, 2008](#)). A recent meta-analysis concluded that modulation of risk processing by potential losses is associated with activation in anterior insula ([Mohr et al., 2010](#)). In DLPFC and PPC, activation is associated with information integration and final decision-making, thereby suggesting specialization within the network supporting decision-making under uncertainty ([Mohr et al., 2010](#)). Our result indicates that the use of the network may depend on individual risk attitudes: In loss-averse subjects, trials with high potential reward triggered stronger risk processing relative to low-reward whereas non-loss-averse subjects engaged in stronger risk processing for trials with low potential reward.

With EV divided into two parametric regressors, losses and gains, we found regional responses to losses that dissociated between loss-averse and non-loss-averse subjects. For the most loss-averse subjects, activation of anterior insula and DLPFC decreased as the absolute size of the loss increased, whereas for the least loss-averse subjects, fronto-insular activation increased as the absolute size of the loss increased. The insula processes somatic information and thereby supports subjective feelings (for a review, see [Critchley, 2005](#)) and its activation is associated with negative emotions such as sadness or anxiety (see [Phan et al., 2002](#), for meta-analysis).

Earlier studies on insular activation and loss aversion are controversial: On the one hand, anticipatory insular activation predicts riskless choices and risk-aversion mistakes ([Kuhnen & Knutson, 2005](#)), correlates with individual susceptibility to the endowment effect ([Knutson et al., 2008](#)), and is stronger when subjects receive

unfair offers in the ultimatum game ([Halko et al., 2009](#); [Sanfey et al., 2003](#)). On the other hand, in [Tom et al. \(2007\)](#), losses were not associated with larger responses in the circuits coding negative affect, such as the insula. Individually different response profiles to losses, as reported here, could well prevent insular activation from being detected in group analysis without loss aversion correlate.

Only in right PPC (angular gyrus) responses to gains differed according to subjects' loss aversion: parametric responses to the size of the gain of a gamble were negative in the least loss-averse subjects and positive in the most loss-averse. Posterior parietal cortex is intimately involved in numerical processing, in particular approximate calculations, rather than exact arithmetics (for reviews, see [Dehaene et al., 2003](#) and [Walsh, 2003](#)). Accordingly, the pattern of parametric responses indicates that loss-averse subjects may have engaged in calculations only when the size of the gain was large while less loss-averse subjects may have accepted such high-gain gambles without calculation.

Subjects who scored high in behavioral inhibition (BIS), that is, in tendency to withdraw in novel situations, accepted fewer gambles and were more loss averse than subjects who scored low in BIS. This accords with the original proposition by [Gray \(1981, 1982\)](#) that the aversive motivational system is sensitive to signals of punishment and nonreward, thus people scoring high on this dimension should show inhibition to behavior leading to potentially negative outcomes, such as risky gambles. Our findings thus highlight how both state-dependent (loss aversion) and trait-like (BIS) variables are associated with risk-taking and the corresponding brain circuitry.

We found that EC modulated the effects of music on loss aversion: relative to disliked music blocks, subjects who scored high in emotional contagion accepted far more gambles while their liked music was playing. Because the EC scale measures how strongly participants 'catch' emotions from their environment, these participants can thus be considered as most sensitive to the effects of the environment's emotional tone has on their decision-making. This kind of "empathic arousal" has previously been suggested as a mechanism driving the emotional effects of music: For exam-

ple, a sad expressions in a piece of music makes the listener mimics the expression (Juslin & Västfjäll, 2008; Scherer & Zentner, 2001).

Activation Elicited by Liked Versus Disliked Music

Independent of brain responses to gambles, the observed superior temporal activation in response to disliked versus liked music varied with emotional contagion scores (see Supplementary material). Subjects with a tendency to 'catch' others' emotions might thus have been susceptible to music-induced emotional modulation of auditory (para)belt areas involved in higher-order auditory processing (Kaas & Hackett, 2000). Future studies that require emotion induction may benefit from self-selected music pieces, for example as gender-neutral cues, facilitating studies that include male and female subjects (unlike for example Knutson et al., 2008 and Yacubian et al., 2006, both with male-only samples).

Conclusions

We conclude that emotional music influences risky decision-making by modulating individuals' risk preferences, which is reflected in expected reward coding in the amygdala and dorsal striatum. Such neural integration could support interactions between preferences for risk and preferences for music. Because emotions adjust an organism's mental and bodily states to cope with adaptive challenges in the environment, automatic emotion-dependent adjustments to risk-taking could facilitate behavior depending on how dangerous versus safe the environment is experienced.

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