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Emotion prediction errors guide socially adaptive behaviour

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People make decisions based on deviations from expected outcomes, known as prediction errors. Past work has focused on reward prediction errors, largely ignoring violations of expected emotional experiences—emotion prediction errors. We leverage a method to measure real-time fluctuations in emotion as people decide to punish or forgive others. Across four studies ($N = 1,016$), we reveal that emotion and reward prediction errors have distinguishable contributions to choice, such that emotion prediction errors exert the strongest impact during decision-making. We additionally find that a choice to punish or forgive can be decoded in less than a second from an evolving emotional response, suggesting that emotions swiftly influence choice. Finally, individuals reporting significant levels of depression exhibit selective impairments in using emotion—but not reward—prediction errors. Evidence for emotion prediction errors potently guiding social behaviours challenge standard decision-making models that have focused solely on reward.

How do we learn to make adaptive decisions, such as whether to avoid a risky financial endeavour or start a collaboration with a new colleague? A rich literature on value-based decision-making illustrates that choices are made based on the expectation of rewards, and that violations of these reward expectations—that is, prediction errors (PEs)—enable an agent to update their knowledge about their environment to facilitate survival[1–4]. Over the last few decades, these insights have been elegantly encapsulated in a reinforcement learning framework[5], which has served as the foundation for virtually all standard models of decision-making. Even complex social behaviours, such as affiliating with coworkers or reconciling with a spouse, are thought to be motivated by the violation of expected outcomes[6,7]. To illustrate, a colleague's failure to meet a deadline might generate a negative PE, which in turn drives learning through continued reinforcement (for example, this colleague is often late to meetings) and adjustments of future behaviours (for example, collaborations with this colleague are to be avoided).

In parallel with research linking reward to decision-making, a separate literature also demonstrates that emotion exerts a powerful influence on choice[8–12]. Although there has been interest in understanding how anticipated emotions affect behaviour[13–18], relatively little work has examined how the violation of expected emotions—a concept we label emotion PEs—influences decision-making, especially in the context of social interactions[19–21]. A person may, for example, avoid collaborating because she dreads interactions with her aloof colleague, only to find out that, once the collaboration begins, her colleague is actually quite warm and humorous. The unexpected joy of working with this colleague therefore produces a positive emotion PE, which motivates more extensive future collaborations. Prior work shows that sophisticated mental models of emotion are used to predict how other people transition between distinct emotional states[22], and predictions about expected aversive emotions such as regret and guilt can shape social interactions[23–25]. However, whether violations of expected emotions also affect decision-making is an open question[19,26].

Additionally, little is known about how reward and emotion relate to one another, as past work on decision-making has either ignored emotional experiences or assumed that emotion is synonymous with reward value[2,27–31]. For example, in a reinforcement learning framework, external rewards (for example, money or juice) are used to update an agent's value function, and any state changes (such as emotions) are considered to be nuisance variables[32]. Other accounts hint that emotions are simply an internal proxy for value, such that emotions may shape how an individual processes the subjective value of a choice by applying a (non-linear) transformation to objective reward[33]. This lack of consensus and clarity impacts the specificity of theories of decision-making and hampers insight into a variety of psychopathologies that are canonically associated with deficits in both reward and emotion processing[34–37]. For instance, it has not been determined whether emotion and reward independently or jointly impact socially maladaptive behaviours accompanying mood disorders, such as depression[38]. Therefore, to gain a holistic understanding of the mechanisms guiding adaptive social decision-making[39,40], it is critical to map the relative contributions of reward and emotion PEs to behaviour.

To test how strongly reward and emotion PEs impact social behaviours such as punishing or forgiving others, we quantify how violations of emotional expectations bias choices in multiple interactive economic games. As a direct analogue to reward PEs, we examine emotion PEs using a framework that treats emotion by its basic psychological constituents free of any implied cognitive structures[41]. This model of emotion partitions emotional experiences into the affective dimensions of valence (pleasurableness) and arousal (alertness/activation)[42,43], which jointly constitute the core affect of emotion (we adopt the term 'emotion PEs', rather than affective PEs, as it captures the conscious emotional experiences participants are being asked to measure and report during these tasks). We developed a technique that measures real-time fluctuations in emotions as the decision process unfolds, enabling us to precisely and mathematically map the subjective experience of emotion alongside economic rewards during social exchanges. This allows us to test the possibility that violations of emotion expectations influence socially consequential choices, such as deciding to punish or forgive a norm violator. In the tradition of

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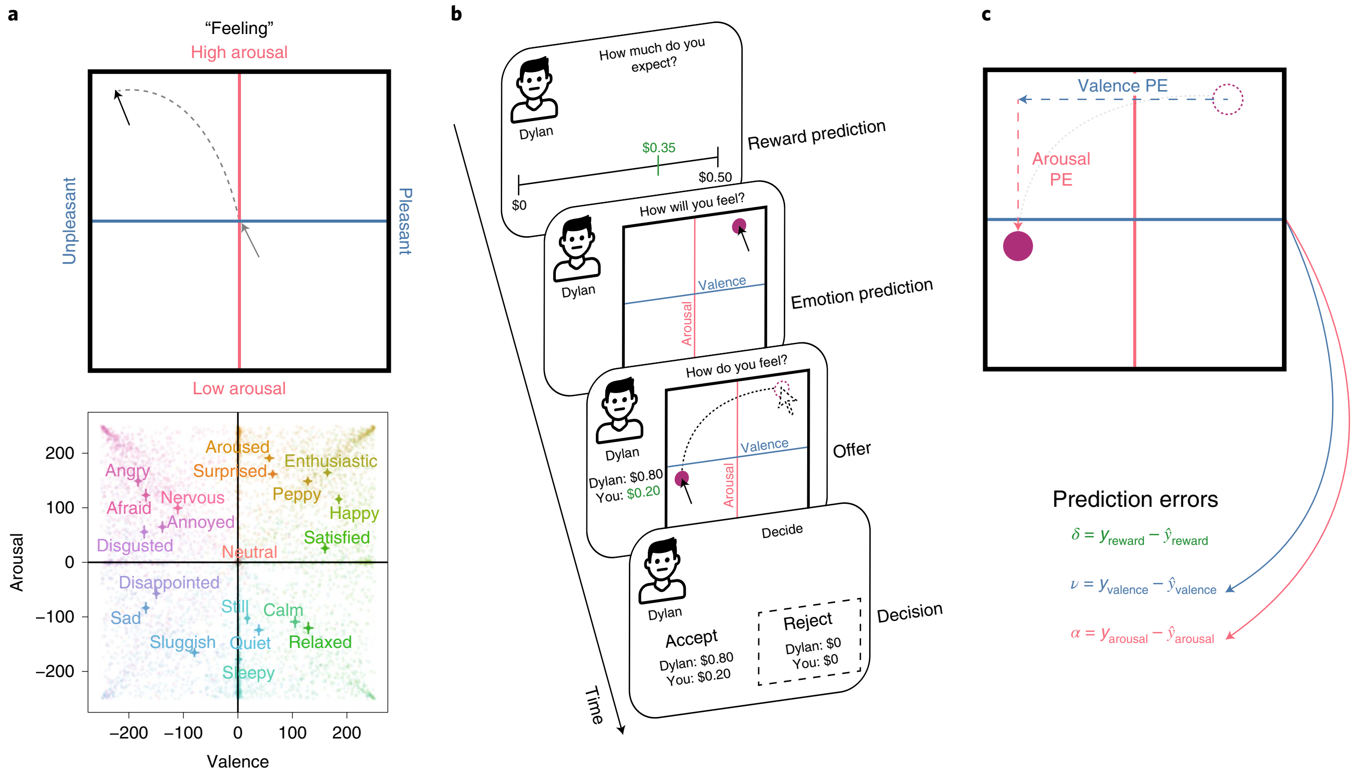

Fig. 1 | The tasks and PE calculations. a, The emotion classification task. Participants rate a series of 20 feelings on the dARM measure, a 500 × 500 pixel grid only delineated by a horizontal (valence axis) and vertical line (arousal axis) along with their labels. The graph below the grid shows the average ratings for 20 feeling words that all participants rated in experiment 1 (each semi-transparent data point reflects one individual rating). Error bars reflect 95% confidence intervals. **b**, The UG trial design. dARM is used in conjunction with the UG to capture emotion expectations and experiences. On each trial, participants make a prediction about how much money they expect to be offered, as well as a prediction about the emotions they expect to experience. Upon seeing the actual offer, participants report their current emotional experience. Finally, participants decide either to accept or to reject the offer. **c**, Calculating reward and emotion PEs. We calculate three trial-level empirical PEs: a reward PE (δ), a valence PE (ν) and an arousal PE (α). In the equations, $\hat{y}$ refers to an individual's prediction about the reward or emotion they would experience, while y refers to their actual experience.

reinforcement learning, we consider reward as an external reinforcer, such as money or food, that encourages similar future behaviours[1,32,44–48]. This allows us to compare the relative strengths of reward and emotion PEs on choice, while remaining agnostic about whether (and/or how) these PEs may eventually be integrated into a common value signal reflecting 'net value'[49].

Across four separate experiments, participants (N=1,016) played one of two behavioural economic games—the Ultimatum Game (UG)[50] or Justice Game (JG)[51]—while simultaneously rating their affective experiences using a measure we term 'dynamic affective representation mapping' (dARM), adapted from the affect grid used in past research[43]. This measure represents a subjective map of emotional responses where the horizontal axis characterizes the valence dimension and the vertical axis characterizes the arousal dimension. A person who is feeling angry might, for example, report high arousal and negative valence by rating their emotional state in the upper-left corner of the grid (Fig. 1a).

In experiment 1, participants (N=364) completed multiple rounds of a one-shot UG online, which captures punitive responses to fairness violations in a dyadic social interaction. Using a between-subjects design, participants played either as the responder or a third-party making decisions on behalf of an anonymous responder. In the UG, the responder received an unfair monetary split from the proposer, and participants were then tasked with deciding whether to accept the proposer's offer as-is or to reject the offer (that is, costly punishment such that neither the proposer nor responder receives any money). In our modified version, participants made ratings on the dARM at two critical time points: first, at the beginning of the trial before there was any monetary offer from the proposer, which captures participants' emotion expectations, and second, after the proposer makes an offer, which captures emotion experience (Fig. 1b). By using the dARM to measure emotions as a social interaction unfolds, we can mathematically compute the difference between emotion expectations and compare them with the actual emotional experience, effectively capturing emotion PEs (Methods). These emotion PEs were measured on two dimensions (valence and arousal), such that a valence PE would be calculated by the difference between the predicted versus experienced (un)pleasantness of the offer, while an arousal PE would be the difference between predicted and experienced arousal (Fig. 1c).

Mirroring how reward PEs are typically treated in the literature[20,52], the effects of reward PEs were captured by having participants make trial-by-trial predictions about the reward they expected to receive from the proposer, which could then be compared with the actual offer received (by subtracting the received offer from the predicted offer). Critically, this design allowed us to distinguish between the contributions of reward and emotion PEs during a dynamic social interaction using the following conceptual model:

$$\text{Choice} \sim \text{Reward PE} + \text{Valence PE} + \text{Arousal PE} \qquad (1)$$

Before examining the extent to which PEs for reward, valence and arousal govern decisions to punish, we scaled all PEs at the group level prior to being modelled (similar to z scoring without mean-centering, as zero is the meaningful case where predictions perfectly match experience), which permitted a direct comparison of their relative contributions to choice using a common metric[53,54].

Results

Emotion and reward PEs have distinguishable contributions to choice. Results reveal that all three types of PE contribute to decisions to punish. Participants punished at higher rates when experiencing less reward or valence than expected, or more arousal than expected (Table 1 and Fig. 2a; the same pattern of results was found using non-parametric regression, see Supplementary Table 3 and Supplementary Fig. 3). A likelihood ratio test demonstrated that the sequential addition of valence ($\chi^2(4) = 512.65, P < 0.001$) and arousal PEs ($\chi^2(4) = 70.24, P < 0.001$) significantly improved the explanatory power of the model over a more traditional analysis which only included reward PEs. Given past work that has characterized emotional valence as a byproduct of reward processing[55–57], it is particularly noteworthy that we find a unique contribution of valence PEs—for example, surprisingly negative feelings such as disappointment or sadness—for punitive decisions. While the valence and reward PEs are correlated at the intra-individual level ($r_{rm} = 0.80, P < 0.001$), the variance inflation factor (VIF) statistics indicate low collinearity between these predictors in our model ($VIF_{valence} = 1.55$, $VIF_{reward} = 1.54$, $VIF_{arousal} = 1.04$) and therefore produce reliable estimates of how strongly these PEs affect choice. Moreover, using a β coefficient test[58], we found that valence PEs have a significantly stronger impact on motivating punitive choices than reward PEs do ($z = -3.74, P < 0.001$). That is, while people do rely on reward PEs to inform their choices, they rely even more on negative deviations from expected emotional valence.

Table 1 | Experiment 1: valence PEs predict decisions to punish better than reward PEs

$\text{Punish}_{i,t} \sim \beta_0 + \beta_1\text{Reward PE}_{i,t} + \beta_2\text{Valence PE}_{i,t} + \beta_3\text{Arousal PE}_{i,t} + \varepsilon$

Variable	Estimate (s.e.)	z	P
Punish			
Intercept	−2.56 (0.18)	−14.26	<0.001***
Reward PE	−1.10 (0.14)	−7.62	<0.001***
Valence PE	−1.92 (0.16)	−11.75	<0.001***
Arousal PE	0.53 (0.09)	5.65	<0.001***

Note that reward PEs are calculated by taking the difference between the experienced and predicted reward. Valence PEs and arousal PEs are calculated by taking the difference between the experienced and predicted emotion. All variables were scaled but not mean-centred, as the zero point on each scale refers to the meaningful instance where participants' expectations matched their experience. The model includes subject-specific random intercepts and slopes for reward PE, valence PE and arousal PE. The dataset includes 7,280 observations from 364 participants. ***$P < 0.001$.

An alternative explanation of these findings is that emotion PEs are merely soaking up the additional variance that would typically be captured by modelling individual differences in the subjective valuation of reward. To test for this possibility, we pitted our empirical PE model against standard utility models that leverage an exponential scaling parameter to capture any non-linear valuations of rewards[33,52,59]. We used the following equations to transform objective reward magnitudes into subjective value before calculating the resulting subjective reward PE (sRPE):

$$\text{sRPE} = \text{reward}^{\lambda}_{\text{actual}} - \text{reward}^{\lambda}_{\text{prediction}} \quad (2)$$

$$\text{where } 0 \leq \lambda \leq 1$$

By bounding λ, this utility model captures the diminishing marginal utility of reward in the tradition of classic utility models[33]. We incorporated sRPEs into a utility model by adding an additional free parameter w_1, which specifies the subject's weight on model-derived sRPEs:

$$\text{utility}_{\text{accept}} = w_1 \text{sRPE} \quad (2.1)$$

$$\text{utility}_{\text{reject}} = 0$$

The choice rule was computed by placing the utility values for each decision into a softmax function:

$$p\,(\text{accept}) = \frac{e^{\beta(\text{utility}_{\text{accept}})}}{e^{\beta(\text{utility}_{\text{accept}})} + e^{\beta(\text{utility}_{\text{reject}})}} \quad (2.2)$$

$$p\,(\text{reject}) = 1 - p\,(\text{accept})$$

Thus, we can compare how our empirically derived PEs (reward, valence and arousal) fare against sRPEs that incorporate non-linear valuation of reward (Supplementary Fig. 4 and Supplementary

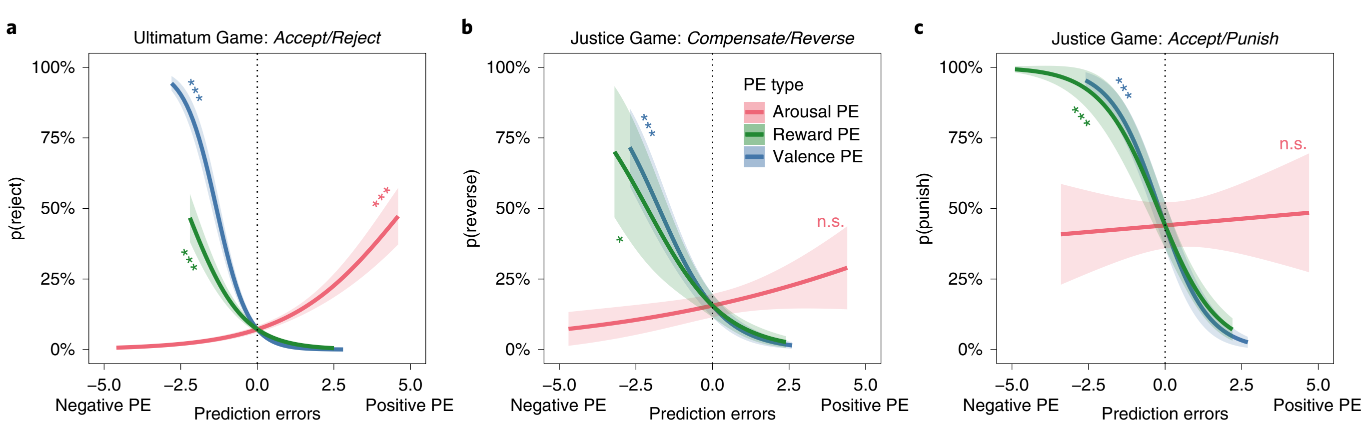

Fig. 2 | Emotion PEs underpin punitive behaviour in the UG and JG. a–c, Participants completed either the UG or JG. The lines on each graph reflect the probability of different choice pairs including rejecting versus accepting in the UG (**a**), reversing versus compensating in the JG (**b**) and punishing versus accepting in the JG (**c**). The colour of each line indicates reward (green), arousal (red) and valence (blue) PEs. Negative values reflect negative PEs, indicating less money (reward), less pleasantness (valence) and less arousal than expected. Shaded areas reflect ±1 s.e. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Table 8). Results reveal that the PE model that includes empirical reward and valence (but not arousal) PEs outperforms all other models, including those that rely on model-derived reward PEs ($t(363) = -15.27$, $P < 0.001$) or other impoverished models that do not account for valence PEs. Furthermore, these results suggest that valence PEs in particular are not merely reflecting individual differences in the subjective valuation of reward.

While the additive model (equation (1)) provides the most direct comparison of the strength of each PE in decisions to punish, we conducted a secondary analysis to assess whether PEs also exert any joint influence on choice. By testing all possible interactions between all three PE types in a mixed-effects regression, we found a significant three-way interaction between reward, valence and arousal PEs ($\beta = -0.37 \pm 0.07$, $z = -4.91$, $P < 0.001$), a significant interaction between valence and arousal PEs ($\beta = -0.36 \pm 0.11$, $z = -3.22$, $P = 0.001$) and between reward and arousal PEs ($\beta = -0.30 \pm 0.11$, $z = -2.65$, $P = 0.008$), but not between reward and valence PEs ($P = 0.60$; Supplementary Table 4). Together, this suggests that the strength of a given PE is partially modulated by other PEs, such that arousal PEs appear to augment the role of valence and reward PEs.

We conducted follow-up analyses to assess the robustness of our results and check for potential non-linearities in the data. First, we tested for non-linear effects of PEs on decision-making using a generalized additive mixed-effects model, which showed that the marginal contribution of valence PEs had a stronger unique contribution to choice than reward PEs (Supplementary Fig. 3 and Supplementary Table 3). Second, we tested the strength of PEs by controlling for expectations (that is, modelling both the prediction and PE in the same regression)[52], which revealed that valence and reward PEs still explain significant variance in decisions to punish, even when controlling for expectations (Supplementary Table 5). Third, we can directly examine the contributions of rewarding and emotional experiences on decisions to punish by fitting a model that only includes information about participants' actual experiences of reward and emotion, independent of their expectations. Results reveal that experienced reward (that is, the offer itself) predicts decisions to punish more strongly than experiences of emotional valence (β comparison: $z = -4.37$, $P < 0.001$) or arousal (β comparison: $z = -10.57$, $P < 0.001$). Finally, since querying emotion predictions directly after reward predictions could have diminished the role of reward PEs, we ran a subsequent pre-registered experiment to replicate our findings while controlling for potential ordering effects (https://osf.io/3mgxz/). In experiment 2 ($N = 228$), there was no evidence that reward PEs were dampened by the presence of asking participants to predict and report their emotional experiences (Supplementary Fig. 7 and Supplementary Tables 9–11). Moreover, as observed in experiment 1, valence PEs had the strongest impact on shaping decisions to punish compared with reward PEs (β comparison: $z = -2.57$, $P = 0.005$).

These results have three important implications. First, reward and emotion expectation violations are distinguishable inputs during decisions to punish. Second, although reward PEs have traditionally been treated as the predominant driver of punitive decisions in social exchanges[3,60], our findings instead indicate that valence emotion PEs are actually the strongest motivator. Third, when considering the direct contributions of experienced reward and emotion, reward appears to more strongly bias behaviour than emotion does, illustrating that emotion only outperforms reward once PEs are considered.

These findings demonstrate a link between emotion PEs and punishment, suggesting that violations of emotion expectations are integral to motivating social choice. It remains unclear, however, how emotions are constructed during the decision-making process, or when these emotional experiences ultimately bias choice. Even when the contributions of emotion are considered alongside reward, emotions are typically treated as a static input rather than a dynamic process[20,61]. This assumption places artificial constraints on the role that emotions play in biasing choice, and is incongruent with theoretical accounts claiming that dynamic fluctuation is a core feature of emotion[16]. Indeed, most major theories of emotion propose that changes in the intensity of experienced affect over time can be integral in shaping behaviours[62,63], and can adaptively vary depending on cue relevant environmental changes[64].

Temporal dynamics of emotion and its relationship with choice. Therefore, to gain a more granular perspective of how emotion biases choice, and to test the robustness of the emotion PE effect observed in experiments 1 and 2, we conducted a third experiment exploring the temporal dynamics of emotion while simultaneously employing a stronger experimental control for the influence of reward on social choice. One of the limitations of using the UG to study dynamic changes in reward and emotion is that each of the options (that is, accept or reject) results in different monetary reward. However, if the relative contribution of reward were experimentally held constant, this would allow us to decouple monetary reward from emotion, and more directly examine how emotion PEs influence choice. Therefore, to control for the variable influence of reward, in experiment 3, participants ($N = 73$) played a modified version of the UG called the JG in a laboratory setting[51]. In the JG, participants always played as the responder and received unfair offers from various proposers. After receiving an offer, responders could redistribute the money between themselves and the proposer. Analogously to the UG, two of the redistribution options were to accept (take the offer as-is) or punish (reduce the proposer's payoff to match the responder's). The JG introduces two additional unique options which capture preferences between non-punitive responses and cost-free punishment: Responders could non-punitively compensate by increasing their own payout to match the amount of money proposers kept for themselves or apply a cost-free punishment by reversing the proposed payoffs, such that proposers get what they offered to responders (Methods). On each trial, only two of the available four options were randomly presented, and participants were never aware which two options would be available. This structure was important for two reasons. First, because there was uncertainty regarding which choice pair participants would receive, the final monetary outcomes were experimentally decoupled from the proposer's original offer. This provided an ideal testbed for studying continuous fluctuations in emotions, as participants' emotions could change over the course of a trial as they received new information about proposers' offers and the possible ways to redistribute the money. Second, by matching the participant's payout by holding reward constant when certain choices were presented together (that is, compensate/reverse and accept/punish), the task structure provides a strong experimental test of how emotion influences social choice independently from the final reward outcome.

As before, we used the dARM to measure participants' emotion predictions about the proposer's offer and emotional experiences after receiving the proposer's offer. Because the available choice pair was unpredictable, we additionally measured participants' emotional experiences after making their decision. All emotion measurements were sampled every 10 ms using mouse tracking, which allowed us to continually measure emotion predictions and experiences as they unfolded in real time.

We first calculated emotion PEs using participants' final emotion rating (mirroring the analysis performed in experiments 1 and 2). Results reveal that negative valence emotion PEs robustly predict choices to punish ($\beta = -1.26 \pm 0.24$, $z = -5.18$, $P < 0.001$) and reverse ($\beta = -0.97 \pm 0.26$, $z = -3.74$, $P < 0.001$). Although significantly predictive of punitive behaviour, these valence emotion PEs did not outperform reward PEs for either choice pair (accept/punish: $z = -0.52$, $P = 0.30$, Fig. 2b; compensate/reverse: $z = -0.43$, $P = 0.34$, Fig. 2c). In contrast to experiments 1 and 2, arousal PEs

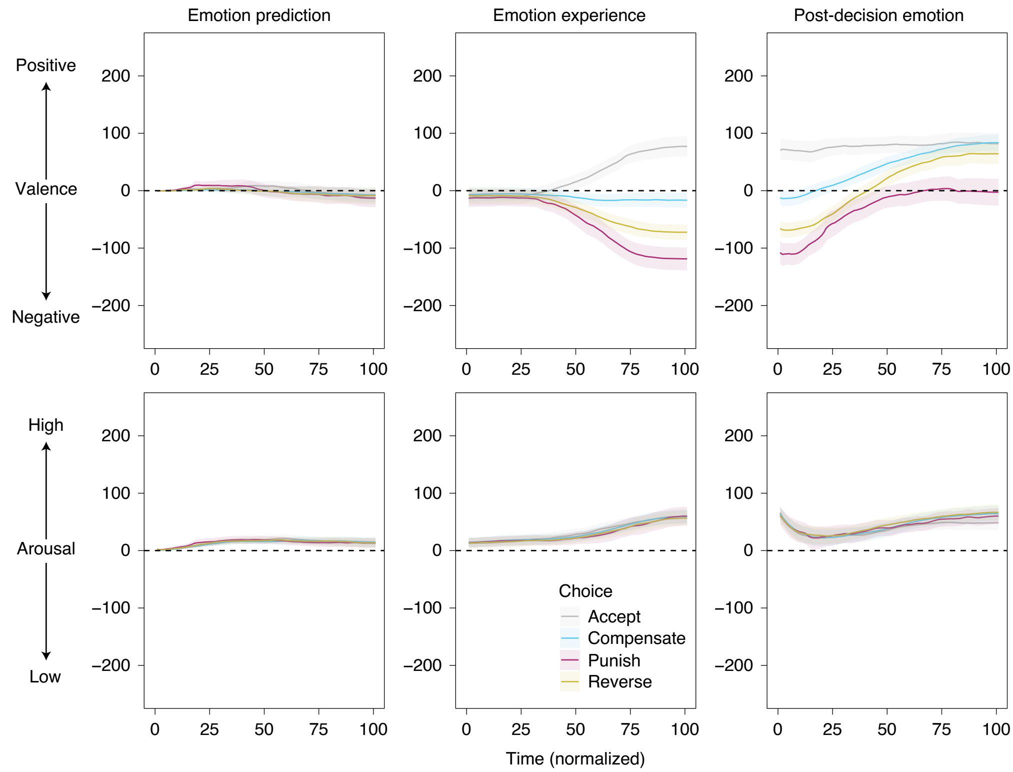

Fig. 3 | Temporal dynamics of emotional experiences during choice. Participants used dARM to continuously report their emotional experiences at every stage of the JG, showing emotion prediction, experience and post-decision emotion. For all measurements, participants' data were normalized for the time it took to make a rating, such that 1 represents the start of the trial and 101 represents the final emotion rating. The average valence and arousal are plotted over time. All shaded areas represent 95% CIs.

were not significantly predictive of decisions to punish or reverse (all P values >0.27; Supplementary Tables 12 and 13), suggesting that the strength of the arousal PE signal may be context dependent. In addition, we tested how these empirically derived PEs fare against subjective (model derived, detailed above in equation (2)) reward PEs. We found that a model that includes empirical reward and valence—but not arousal—PEs outperforms all other models, including those that only rely on model-derived reward PEs ($t(72) = -49.7$, $P < 0.001$; Supplementary Fig. 8 and Supplementary Table 15). Taken alongside the results from experiments 1 and 2, these findings suggest that emotion PEs—and in particular valence PEs—play a unique role in biasing various types of social choices, are at least equally potent as reward PEs in motivating social behaviours and can be more powerful than reward PEs in certain contexts.

To further examine how the construction of emotion biases choice, we probed real-time fluctuations in participants' emotional experiences. Participants were permitted to report their emotional experiences at their own pace, resulting in trials of different lengths. We therefore resampled all emotion trajectories to a normalized timescale consisting of 100 time points to aid interpretation[65], then averaged participants' emotional responses across choices. Figure 3 shows the unique emotion trajectory across time, separately for valence and arousal, for any given decision (accept, punish, reverse or compensate). When comparing the emotional trajectories in compensate versus reverse trials only, results reveal that participants' eventual decisions to reverse an unfair offer—a retributive eye-for-an-eye response—can be predicted by the 37th time point on the normalized scale, which corresponds to 1.65 s on an absolute timescale. Early emotional trajectories were so potent that we could even predict some decisions as early as half a second on an absolute timescale (for the accept/compensate pair with a moderately unfair offer; Supplementary Table 16). We also examined how individuals' choices alter their emotions after the social interaction. While on average everyone's emotional valence increased after making a choice, those who responded punitively (reverse or punish) rapidly reported feeling positive emotional valence (Fig. 3)—a 'joy of punishment' effect. Together, these results reveal that, by experimentally stripping away the potential influence of monetary reward on choice, there is a striking impact of early emotional experiences on guiding which subsequent choice is taken—which provides further evidence that reward and emotion have unique inputs to social choice.

Functional dissociation between reward and emotion PEs. The privileged role of emotion PEs in guiding social behaviour has important implications for mood disorders such as depression, which is often characterized by impairments in both reward and emotion processing[36]. To date, however, extant research on depression has examined reward and emotion in a siloed manner[66,67]—that is, they have not been interrogated side-by-side within the same paradigm—and there have been few attempts to link them to decision-making in lockstep. Consequently, it remains unclear whether reward or emotion deficits are the primary contributor to symptoms and socially maladaptive behaviours seen in clinical populations, such as anhedonia[35] and avolition[68]. We therefore conducted a pre-registered fourth experiment (https://osf.io/qfejk/) comparing healthy controls against individuals reporting significant levels of depressive symptoms.

Experiment 4 ($N = 351$) measured participants' predictions and experiences about reward and emotion in the UG. After completing the task, participants completed questionnaires indexing various mood disorders, including the Center for Epidemiologic Studies

Table 2 | Experiment 4: individuals at risk of depression are less sensitive to unfairness

$$\text{Punish}_{i,t} \sim \beta_0 + \beta_1\text{Depression}_i + \beta_2\text{Unfairness}_{i,t} + \beta_3\,(\text{Depression} \times \text{Unfairness})_{i,t} + \varepsilon$$

Variable	Estimate (s.e.)	z	P
Punish			
Intercept	−4.57 (0.48)	−9.56	<0.001***
Depressed	1.42 (0.60)	2.38	0.018*
Unfairness	5.57 (0.38)	14.53	<0.001***
Depressed × unfairness	−1.80 (0.42)	−4.24	<0.001***

Note that unfairness is scaled and mean-centred. Depression is a binary variable with healthy controls (0) and those at risk of depression (1). The model includes subject-specific random intercepts and slopes for unfairness. The dataset includes 7,020 observations from 351 participants. *P < 0.05, ***P <0.001

Depression Scale (CES-D)[69]. Participants were classified as at risk for depression or a healthy control based on scoring guidelines of depression symptomatology of the CES-D (see Methods for details about the CES-D and all additional measures).

We first observed that, compared with healthy controls, those at risk for depression were less sensitive to offer unfairness, which led them to be more punitive for fair offers and less punitive for unfair offers (Table 2). Given these observed behavioural differences, our primary goal was to then examine whether participants at risk for depression demonstrated aberrant use of reward and/or emotion PEs when deciding to punish. Replicating our findings from the first three experiments, healthy controls (N = 205) relied most heavily on valence PEs when making punitive decisions (β = −2.08 ± 0.29, z = −7.15, P < 0.001). Valence PEs were also more predictive of decisions to punish than reward PEs were (β = −1.41 ± 0.23, z = −6.03, P = < 0.001; β coefficient test: z = −1.80, P = 0.036; Fig. 4a). In contrast, individuals at risk for depression (N = 146) demonstrated no reliance on arousal PEs (β = 0.01 ± 0.13, z = 0.09, P = 0.93) and significantly more reliance on reward compared with valence PEs (reward: β = −1.43 ± 0.18, z = −7.79, P < 0.001; valence: β = −0.94 ± 0.16, z = −5.81, P < 0.001; β coefficient test: z = −1.98, P = 0.02; Fig. 4a)—which accords with previous work showing that people with depression exhibit intact reward PEs in certain contexts[70].

Using the healthy controls as a benchmark, those at risk for depression exhibited selective impairment in their use of both emotion PEs when punishing, but there were no observable differences in reward PE processing. Remarkably, the attenuated reliance on valence and arousal PEs led to less punishment of a transgressor compared with healthy controls (Table 3 and Fig. 4b). While it is possible that participants at risk for depression could simply have less reliable emotion PEs, this explanation is unlikely given the nearly identical distribution of arousal and valence PEs between groups (Supplementary Fig. 13). These findings reveal a functional dissociation between emotion and reward during the decision-making process in depression, suggesting that the two may be cognitively separable.

To further probe why participants at risk of depression relied less on emotion PEs, we next examined participants' responses in an independent emotion classification task. In this task, participants rated 20 canonical emotion labels (for example, anger) on the dARM, which required them to draw upon their past memories and knowledge of how they experience each of these emotions (Methods). Results reveal that individuals classified as at risk for depression have a smaller range of emotional experiences (Welch two-sample t-test: t(263.34) = 4.33, P < 0.001, Hedge's g = 0.49; Fig. 4c,d). Restricted emotion representations were observed along both the valence and arousal dimensions. This suggests that depression may be linked with impairments in how emotional experiences are represented[71,72], and may help explain why depression attenuated the influence of emotion PEs on decisions to punish in our experiment.

Discussion

Historically, there have been two major perspectives concerning the relationship between emotion, reward and decision-making. Either emotion has been considered irrelevant or purely incidental to choice, or else emotion and reward have been treated as so intrinsically intertwined that they cannot be disentangled, thus serving similar functional roles[27–29,31]. Here, we examine the relationship between emotion and reward, revealing that neither of these accounts is accurate. By classifying emotions into distinct affective components (valence and arousal), we interrogated the possibility that emotion and reward PEs make both unique and interactive contributions to socially consequential choices, such as punishing or forgiving moral transgressors. Our findings document that people rely heavily on violations of their emotional expectations to make social decisions, and that these emotion PEs are just as powerful, if not more potent, than reward PEs in guiding social behaviours.

By mathematically computing the consciously accessible affective states using the dARM, we were able to measure PEs for different dimensions of emotion[43], explore whether specific types of expectation violations are especially consequential for social decisions and broaden the scope of research on anticipated emotion by creating a generalizable framework that does not rely on discrete emotions such as guilt or regret[73]. These findings build on a rich literature documenting how decision-making is influenced by emotion[8,9,11,12,28]. We demonstrate that negative valence PEs (negative surprise) and positive arousal PEs (experiencing more arousal than expected) increase the likelihood of punishing, such that valence and arousal PEs have independent and opposite effects on choice. We note, however, that the influence of arousal PEs on choice appears to be context dependent, as we did not observe an effect of arousal PEs in experiment 3. In contrast to past accounts[20,28], these results imply that emotions ought to be considered in relation to the violation of an emotional expectation—not just in the emotional experience itself.

Even when the emotional experience is considered in isolation, methodological advances measuring moment-to-moment emotional changes can document the real-time evolution of how this process unfolds, clarifying emotion's role in social decision-making. For example, we find that early emotional reactions—those that come online in less than a second during the social interaction—quickly and powerfully predict which social choices people subsequently make. Furthermore, the choices that people make can drastically influence their emotional states: Choosing to punish perpetrators results in a rapid positive boost ('a joy of punishment') in the wake of their decision. Together, these results accord with a growing literature on predictive processing[74] and suggest that early, transient emotional states during an unfair social exchange are essential in governing whether people ultimately decide to punish or forgive a perpetrator.

By adopting a PE framework to explore how social decisions are shaped by violations of emotional expectations, we were able to compare the strength of reward and emotion PEs in motivating decisions to punish and help others. Foundational work in decision-making has focused on rewards as external reinforcers, illustrating that reward PEs are an important mechanism for enabling adaptive behaviour, as they allow people to compare their expectations against their experiences to modify actions accordingly[1,3]. We observe this in our own studies. Reward PEs explain significant variation in social behaviours and critically contribute to

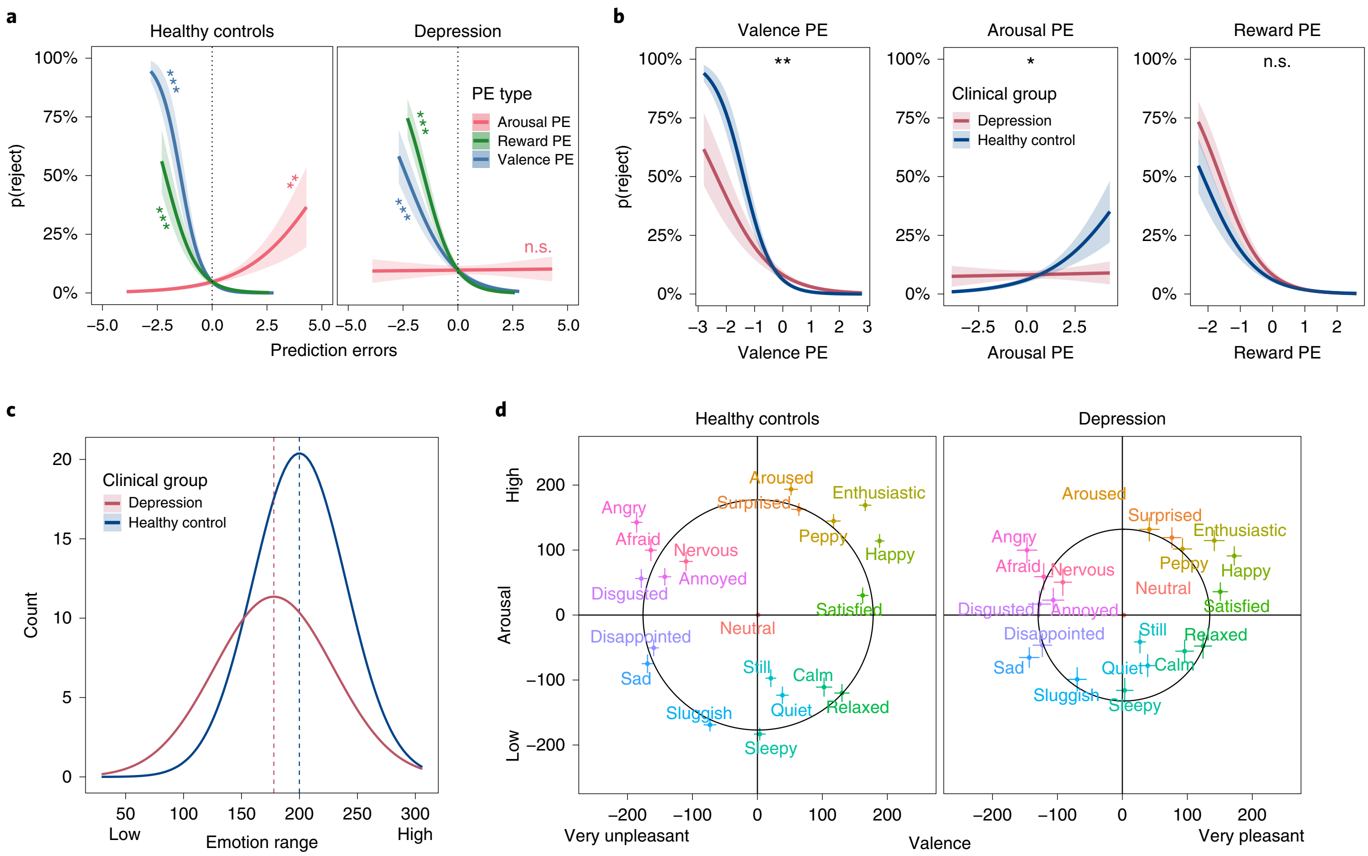

Fig. 4 | Results of experiment 4. a, PE use in healthy controls and those at risk for depression. The probability of rejecting the offer is plotted for all three types of PEs (reward, arousal and valence) for healthy controls (left) and those reporting significant levels of depression (right). Negative values reflect negative PEs, while positive values reflect positive PEs. Analyses represent separate regression effects. Shaded areas reflect ±1 s.e. **b**, PEs plotted by group. The use of each PE is plotted for both healthy controls and individuals at risk of depression. Analyses represent interactions between each PE and group. **c**, Emotion range. Each participant's emotion ratings were used to calculate the average distance of their ratings from neutral (that is, the radius of their unique circumplex), thereby indexing their emotional range. Histograms represent normal distributions for both groups, and dashed lines indicate their respective means. **d**, Group-level average emotion ratings. Participants rated 20 typical emotions using the dARM. Circles represent emotion range fits for each group. Error bars represent 95% CIs. Shaded areas reflect ±1 s.e. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

the choices people make during social interactions. In a similar vein, people rely on violations of their emotional expectations to calibrate their choices, and we observed a particularly robust role of valence PEs in predicting social choices across contexts. Arousal PEs, on the other hand, seem to be more sensitive to social context, as they were not universally deployed across all experiments (that is, the arousal PE effect was not observed in the JG, and once predictions were accounted for in the UG, arousal PEs no longer provided significant predictive value). Our computational model further hints that, regardless of context, some individuals may not rely on arousal PEs at all to inform their choices. When taken together, our results suggest that the different types of PEs uniquely and interactively contribute to social choice, such that neither emotion nor reward predictions alone tell the whole story. Rather, social choices appear to be the result of joint inputs from both emotion and reward PEs.

These findings are compatible with the theory that value is neurally encoded as a common currency, where the value of choice options under consideration is mapped to a single scale for comparison[49,75]. For example, the multiple different types of PEs measured in our studies—reward, valence and arousal—may feed into an integrated value signal in the prefrontal cortex[76,77]. It additionally remains unknown whether a common value representation places equal weight on each kind of PE, or whether value is asymmetrically biased by valence PEs. Future work could help clarify how (and where) these distinct emotion and reward PEs are processed in the brain and the extent to which they are separable.

The adaptive qualities of emotion PEs become readily apparent when considering people at risk for depression, who were selectively impaired in using emotion—but not reward—PEs when making social decisions. We observed that individuals reporting significant levels of depression exhibited attenuated use of valence PEs and did not rely on arousal PEs at all, which led to less punishment of a norm transgressor. In contrast, they exhibited fully intact use of reward PEs, which accords with past research[78] (although this may be contingent on the learning context; cf. refs. [79–81]). This pattern of relying on emotion PEs rather than reward PEs seems central to healthy and adaptive social decision-making. Depression was associated with a reduced range of emotional responses in our studies, highlighting that emotional processes are fundamentally altered in mood disorders[71,82]. This emotional constraint may help explain the aberrant use of emotion PEs in those suffering from depression. Put simply, if a person is less sensitive in distinguishing between affective states, then they may be less able to choose appropriate actions given the social dynamics of the situation.

For close to a century, psychologists have sought to understand the essential drivers of human behaviour. One successful framework, reinforcement learning, has elegantly illustrated that people make consequential decisions based on violations of expected

Table 3 | Experiment 4: individuals at risk of depression have selective impairment in emotion (but not reward) PEs

$$\text{Punish}_{i,t} \sim \beta_0 + \beta_1 \text{rPE}_{i,t} + \beta_2 \text{vPE}_{i,t} + \beta_3 \text{aPE}_{i,t} + \beta_4 \text{Depression}_i + \beta_5 (\text{rPE} \times \text{Depression})_{i,t} + \beta_6 (\text{vPE} \times \text{Depression})_{i,t} + \beta_7 (\text{aPE} \times \text{Depression})_{i,t} + \varepsilon$$

Variable	Estimate (s.e.)	*z*	*P*
Punish			
Intercept	−2.73 (0.22)	−12.58	<0.001***
Reward PE	−1.27 (0.19)	−6.54	<0.001***
Valence PE	−1.96 (0.22)	−9.03	<0.001***
Arousal PE	0.49 (0.14)	3.58	<0.001***
Depression	0.31 (0.30)	1.04	0.296
Reward PE × depression	−0.22 (0.25)	−0.88	0.378
Valence PE × depression	0.93 (0.29)	3.24	0.001**
Arousal PE × depression	−0.47 (0.18)	−2.54	0.011*

Note that reward PEs are calculated by taking the difference between the experienced and predicted reward. Valence PEs and arousal PEs are calculated by taking the difference between the experienced and predicted emotion. All variables were scaled but not mean-centred, as the zero point on each scale refers to the meaningful instance where expectations match experiences. Depression is a binary variable with healthy controls (0) and those at risk of depression (1). The model includes subject-specific random intercepts and slopes for reward PE, valence PE and arousal PE. The dataset includes 7,020 observations from 351 participants. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

rewards. This canon of work has laid the building blocks of how we understand human learning and decision-making. By adopting a similar approach, we reveal that violations of emotional expectations—emotion PEs—play an outsized role in guiding social behaviours. Using a variety of multimodal techniques, we document consistent evidence that these emotion PEs exert a strong influence on social behaviours, above and beyond reward PEs. Although past research has often placed reward PEs at the heart of decision-making, our results instead suggest that people robustly use violations of their emotional expectations to make decisions that influence both themselves and others. Contrary to conventional wisdom, we find that the only time reward plays a stronger role than emotion in decision-making is when experiences are considered in isolation from expectations. Together, these results highlight the critical importance that violations of expected emotions play, suggesting that emotional processes are just as consequential—if not more so—than violations of reward for guiding social behaviours.

Methods

Participants. Across all four experiments, participants ($N = 1{,}225$) received either monetary compensation or partial course credit, and provided informed consent in a manner approved by Brown University's Institutional Review Board under protocol 1607001555. In experiment 1, we aimed to collect a sample of 350 participants, which exceeds the sample sizes used in similar paradigms using reward PEs to study decision-making in the UG[20,21]. We recruited 398 individuals online using Amazon Mechanical Turk (AMT). To protect against data contamination from bots posing as real participants[83], we excluded 34 individuals' data using a conservative measure of non-compliance on the emotion classification task, which involved correctly rating the 'neutral' feeling that we explicitly instructed ought to be in the centre of the dARM (Supplementary Methods). This resulted in a final sample of 364 participants (172 female; mean age 33.77 years, s.d. 9.97 years). In experiment 2, we collected 244 participants and excluded 16 individuals due to non-compliance, resulting in a final sample of 228 participants based on our pre-registration (127 female; mean age 35.30 years, s.d. 11.8 years; Supplementary Information). In experiment 3, we recruited 75 individuals and excluded 2 individuals due to non-compliance, resulting in a final sample of 73 participants (39 female; mean age 20.33 years, s.d. 3.27 years), comparable to similar paradigms using the JG[51]. In experiment 4, we aimed to collect a sample of 150 participants at risk of depression using AMT, as detailed in our pre-registration report, and we accordingly recruited a total of 508 participants. Using the pre-registered exclusion criterion (identical to the one used in experiment 1), we excluded 157 individuals from analysis due to non-compliance, resulting in a final sample of 351 participants (149 female; mean age 35.13 years, s.d. 10.21 years) with 205 healthy controls and 146 individuals classified as at risk of depression.

General procedure. In all experiments, participants used the dARM measure to rate their emotion experiences in real time during an emotion classification task and a behavioural economic game. After completing these tasks, participants responded to a series of individual measures and/or clinical battery, depending on the experiment.

dARM measure. In experiments 1, 2 and 4, we collected data using the Qualtrics online survey platform. Adapted from the affect grid used in past research[43], participants were presented with the dARM measure with a sampling resolution of 500 × 500 pixels, and asked to make their affective rating by clicking anywhere in the grid space. This enabled us to simultaneously capture fine-grained self-reports of both the valence and arousal dimensions. To familiarize participants with the use of the dARM, all participants first completed an emotion classification task. In this task, participants were asked to make ratings of 20 canonical emotion words on the grid (for example, angry, sad and surprised) in a randomized order. While this affective representation is typically inferred from pairwise similarity ratings of discrete emotions[84], simply training participants to interpret this subjective map has shown strong convergent validity with other approaches for emotion ratings[43]. To capture real-time mouse tracking in experiment 3, which was run in the laboratory, we used the Psychtoolbox library in MATLAB to implement the dARM with a spatial resolution of 500 × 500 pixels and a temporal resolution of 10 ms sampling. All participants first completed the emotion classification task.

Tasks. In experiment 1, participants played 20 rounds of the UG as either the responder or a third-party. Since responders and third-party deciders reacted to unfairness in similar ways, we collapsed across role for this analysis (Supplementary Table 2). On each trial, participants were asked to answer the following questions: (i) Predict how much reward the responder would get (that is, how much the proposer would offer), within a range of \$0 to \$0.50; (ii) Predict what emotions they expected to feel based on that reward; (iii) Report their actual emotion experience upon receiving the offer; and (iv) Decide whether to accept or reject the proposer's offer. The unfairness of the offer was drawn from a pseudo-random uniform distribution such that participants saw the full range of fair (\$0.50, \$0.50) to unfair (\$0.95, \$0.05) offers.

In experiment 2, participants played 20 rounds of the UG as the responder. All participants completed two blocks in a counterbalanced order, a reward-only block and a reward + emotion block. In the reward-only block, participants only made reward predictions without any emotion predictions or emotion experience ratings. The reward + emotion block design was the same as experiment 1.

In experiment 3, participants played the JG in the laboratory. In the JG, participants always play as the responder and are paired with a unique anonymous proposer on every trial, who offers the responder a split of money. On each of the 54 trials, the two options presented to the responder are drawn randomly from the four available options, ensuring that participants do not know what their choice set will be ahead of time. The four available options are: (1) accept: keeps the offer as-is; (2) punish: reduces the payout of the proposer to what was offered to the responder; (3) compensate: increase the responder's payout to match the proposer's; and (4) reverse: swaps the payouts. For example, using the notation (\$proposer, \$responder), if the offer was highly unfair (\$9, \$1), the four options would be accept (\$9, \$1), punish (\$1, \$1), compensate (\$9, \$9) and reverse (\$1, \$9). The unfairness of the offer was generated such that low, medium and high unfair offers were equally likely and each offer was generated using a truncated normal distribution (the proposer kept \$5.10–6.30 for low offers, \$6.90–8.10 for medium offers and \$8.70–9.90 for high offers). Participants were asked to do the following on a trial-by-trial basis: (i) predict how much reward they would receive,

(ii) predict what emotions they expected to feel based on that reward, (iii) report their emotional experience upon receiving the proposer's offer and (iv) make a decision about how to redistribute the money. Participants were also asked to report their emotional experience after making a decision, to capture changes in their affective state depending on the available redistribution options. Because there were only 54 trials with six unique choice pairs and three levels of unfairness, time course analyses examining specific choice pairs (for example, compensate/reverse) only include nine trials per subject.

In experiment 4, participants played 20 rounds of the UG as the responder. Otherwise, the UG design in experiment 4 was identical to experiment 1.

Post-task questionnaires. Following these tasks, participants completed a series of individual difference questionnaires. In experiments 1 and 4, we collected two survey measures for use as potential covariates: the Emotion Regulation Questionnaire[85] and the 20-item Toronto Alexithymia Scale[86]. In experiment 4, participants also completed the CES-D[69] and five survey measures to index how richly they experience reward and emotion: the Temporal Experience of Pleasure Scale[87], the Behavioral Inhibition and Behavioral Activation Scales[88], the Snaith–Hamilton Pleasure Scale[89], the Apathy Evaluation Scale[90] and the 20-item Toronto Alexithymia Scale[86]. The primary measure of importance was the CES-D, as it allowed us to identify which participants were at risk of depression. Our hypotheses and predictions about all measures were pre-registered and can be found in our OSF pre-registered report (https://osf.io/qfejk/). Analyses of the other measures are included in the Supplementary Information.

Analysis. Across all experiments, we used logistic mixed-effects regressions to predict participants' decisions using the lme4 package in R (ref. [91]). All PEs were calculated by taking the difference between the participants' experience (at the time of offer) and the participants' prediction (before the offer). To ensure that the β coefficients from logistic regressions were comparable, we scaled (but did not mean-centre) all PEs before entering them into the regression. We chose not to mean-centre the PEs because zero indicates meaningful cases in which the participant's prediction matched their experience, therefore producing no error.

In experiments 1 and 2, we used valence PEs, arousal PEs and reward PEs to predict prosocial decisions to accept or punitive decisions to reject. The same regression specification was carried forward in all experiments. In experiment 3, we emulated experiment 1's analysis by taking the endpoints of the participants' mouse trajectories (that is, the final valence and arousal ratings) to run separate logistic mixed-effects regressions for the accept/punish choice set and the compensate/reverse choice set. The regression for experiment 4 additionally included terms accounting for being classified as in the depressed or healthy control group (based on CES-D scores), and the interactions between depression and all PE variants. To aid interpretation, we additionally performed separate regressions for participants who had significant levels of depressive symptoms and those who did not (that is, a binary variable based on a CES-D threshold of 16, according to scoring guidelines).

To analyse real-time fluctuations in participants' emotions in experiment 3, we discretized the time data into 10 ms bins (that is, our sampling rate). Because participants' emotional ratings were self-paced and had variable response times, we normalized each participants' response time on a trial-by-trial basis to compare across participants. Accordingly, participants' response times were rescaled from 1 (start of trial) to 101 (participant clicked response)[92,93]. Participants' valence and arousal measurements were averaged within each normalized time bin, allowing us to directly compare the distribution of valence and arousal responses for each of the choice sets (accept/punish and compensate/reverse) using one-way ANOVAs at each normalized time bin. To use a principled way of defining significant clusters of time bins, we used cluster-based permutation testing, which controls for multiple comparisons by generating null distributions of clusters that can be compared against true clusters[94–97]. This method estimates how big clusters would be if there would no differences between the groups (for example, decisions to compensate or reverse). Permutation tests assume that these observation labels are exchangeable under the null hypothesis, such that, if there is no difference between the groups, then the labels can be randomly shuffled without consequence. For each randomly permutated time series, the largest cluster statistic is calculated (the summation of F statistics for the largest temporally continuous cluster), which represents the largest cluster that could appear due to chance. After repeating this process 1,000 times (which builds a null distribution of clusters), we test whether the clusters observed in our data are greater than 95% of the clusters expect by chance. This ensures we can precisely quantify how the evolution of emotions affects later decisions to be punitive or forgiving while controlling for multiple comparisons.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Experiment materials information and all experiment de-identified data are publicly available at https://github.com/jpheffne/epe. The materials used in this study are widely available.

Code availability

Data analysis script notebooks are publicly available at https://github.com/jpheffne/epe.

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Author contributions

J.H., J.-Y.S. and O.F.H. contributed to designing the research and writing the paper. J.H. analysed the data.

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The authors declare no competing interests

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Software and code

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Data collection	Data for Experiments 1 and 4 were collected using web-based surveys implemented on Mechanical Turk while Experiment 2 was collected from Prolific. Data for Experiment 3 was collected using Psychtoolbox 3 in Matlab.
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Behavioural & social sciences study design

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Study description	Data are quantitative. All experiments are experimental.
Research sample	The research samples for experiments 1, 2 and 4 consisted of workers from Amazon's Mechanical Turk. While not a fully representative sample, the participants are more diverse in age, race, and socioeconomic status than typical undergraduate research samples (Buhrmester, Kwang, & Gosling, 2011; Perspectives on Psychological Science). See demographic information below. The research sample for Experiment 3 consisted of undergraduates at the local university.
Sampling strategy	All experiments used random sampling. In experiment 1, we aimed to collect roughly 350 participants to exceed sample sizes of past studies using the same economic game. We collected 398 Mechanical Turk participants and 34 participants were excluded for not following instructions, ending in a final sample of 364. In experiment 2, we replicated and extended experiment 1 and aimed to collect 215 participants from Prolific which was sufficient for a replication (as detailed in our preregistration https://osf.io/3mgxz). We collected 244 participants and excluded 16 individuals due to noncompliance, resulting in a final sample of 228 participants. In experiment 3, we used a different experimental task and aimed to collect roughly 75 participants in a laboratory setting at the local university, which exceeds sample sizes of past studies using the same economic game. Two participants were excluded for not following instructions, resulting in a final sample of 73. In experiment 4, we aimed to collect 150 Mechanical Turk participants with depression (as detailed in our preregistration report https://osf.io/qfejk/) and we accordingly collected a total of 508 participants. Using the preregistered exclusion criterion (identical to the one used in Experiment 1), we excluded 157 participants due to noncompliance, resulting in a final sample of 351 participants (205 healthy controls, 146 individuals with clinically-significant depression).
Data collection	All data were collected in computer-based experiments, which measured participants responses, response times, and in Experiment 3, mouse trajectories.
Timing	Experiment 1 data was collected from 8/28/2017 to 10/30/2017. Experiment 2 was collected from 6/16/2020 to 6/23/2020. Experiment 3 data was collected from 9/10/18 to 12/10/18. Experiment 4 data was collected from 4/23/2019 to 4/24/2019.
Data exclusions	In all 4 experiments participants were excluded based on our noncompliance policy described in our preregistration report (withheld for double blind review). This conservative measure of noncompliance required participants to correctly rate the 'neutral' feeling in the emotion classification task, which we explicitly instructed participants to rate in the center of a 500 x 500 pixel square (dARM). If participants neutral rating fell outside of a 50 x 50 square around the center, then they were excluded.
Non-participation	No participants dropped out or declined participation.
Randomization	In all Experiments no between-subjects experimental groups were created.

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Population characteristics	Experiment 1: n = 364 (172 female; mean age = 33.77; SD = 9.97); Experiment 2: n = 228 (127 female; mean age = 35.30, SD = 11.8). Experiment 3: n = 73 (39 female; mean age = 20.33; SD = 3.27); Experiment 3 n = 351 (149 female; mean age = 35.13; SD = 10.21).
Recruitment	Participants in Experiments 1 and 4 were recruited from Amazon's Mechanical Turk user base. Participants from Experiment 2 were recruited through Prolific user base. The only restrictions placed on the sample were age (above 18), nationality (born and raised in the United States), and an "approval rate" (indicating that the participant pays attention and follows instructions

correctly in tasks) of over 95%. While all participants are self-selected due to interest and motivation to participate in research studies, this is unlikely to introduce bias into the sample since the participants are more diverse in age, race, and socioeconomic status than typical undergraduate research samples (Buhrmester, Kwang, & Gosling, 2011; Perspectives on Psychological Science), and studies have shown that MTurk workers provide high-quality data that replicates many classic findings in experimental psychology (Piolacci & Chandler, 2014; Current Directions in Psychological Science).

Participants in Experiment 3 were recruited from the local university's participant pool. Participants are undergraduates and are self-selected due to interest and motivation to participate in research studies.

Ethics oversight	The study protocol was approved by the local university's Institutional Review Board.

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