Affective biases encoded by the pupil-linked central arousal systems dynamically modulate inequality aversion in human interpersonal negotiations

Daniel AJ Murphy[1,2], Catherine J Harmer[3], Michael Browning[3,4], Erdem Pulcu[3,4]*

[1] University of Oxford Medical School

[2] St George's, University of London

[3] University of Oxford, Department of Psychiatry

[4] Oxford Health NHS Foundation Trust, Oxford, UK

***Correspondence:**

Dr. Erdem Pulcu

Department of Psychiatry, Neurosciences Building, Computational Psychiatry Lab

Warneford Hospital OX3 7JX

Oxford / United Kingdom

email: erdem.pulcu@psych.ox.ac.uk

Abstract

Negotiating with others about how finite resources (e.g. achievement-based rewards) should be distributed is an important aspect of human social life. However, little is known about computational and physiological mechanisms underlying human social interactive decision-making. Here, we report results from a novel iterative Ultimatum Game (UG) task, in which the proposer's facial emotions and offer amounts were sampled probabilistically based on the participant's (acting as the responder) decisions, creating a gradually evolving social interactive decision-making environment. Our model-free results confirm the prediction that both the proposer's facial emotions and the offer amount influence participant choice behaviour. These main effects clearly demonstrate that human choice behaviour violates the assumptions of the Rational Actor model (the optimal economic strategy for the UG) which posits that all offers should be accepted irrespective of the offer size and the proposer's facial emotions. Model-based analyses extend these findings and demonstrate that participants use an inequality aversion model while computing decision values in the UG. We highlight that the proposer's facial responses to participant decisions dynamically modulate how human decision-makers perceive self—other inequality, relaxing its otherwise negative influence on decision values. In iterative games, this cognitive model underlies how offers initially rejected can gradually become more acceptable under increasing affective load, and accurately predicts 83% of participant decisions. Activity of the central arousal systems, assessed by measuring pupil size, encode a key element of this behavioural model: proposer's affective reactions in response to participant decisions, which dynamically modulate perceived self—other inequality. We further demonstrate that a surprise response, estimated by a recursive Bayesian filter, is associated with pupil dilation and attenuates participants' acceptance probability. Taken together, our results demonstrate that, under affective load, inequality aversion is a malleable cognitive process which is modulated by the activity of the pupil-linked central arousal systems.

Keywords: Ultimatum game, computational modelling, emotional processing, social decision-making, pupillometry, neuroeconomics

Introduction

Negotiating with other people for one's own share of finite resources is an important part of human social-economic life. Recent historic events (e.g. "trade wars" between the United States and China, Brexit negotiations between the European Union and the United Kingdom[1,2]) further highlight this importance, wherein the outcome of negotiations between only a handful of people will directly affect the lives of many others. However, computational and physiological mechanisms of such iterative social interactive decision processes remain mostly elusive.

The Ultimatum Game (UG) is a common behavioural economic measure which is used as an experimental probe of social interactive decision-making processes between two parties. In a recent study, we showed novel evidence to suggest that *proposers* use a risky decision-making model to navigate around violating *responders*' fairness threshold. Proposers were shown to maximise their gains by choosing between Ultimatums based on their expected values, while taking probability of rejection into account[3]. Rejecting an unfair proposal in the UG is also framed as a form of altruistic punishment [4-6], as a responder rejecting an offer sacrifices the amount of money offered to them at the expense of conveying [an implicit] message to the proposer that the amount offered had been *unfair*. This is because both the proposer and the responder receive nothing when an offer is rejected in the UG. Consequently, the responder's rejections in the UG violate the assumptions of the Rational Actor Model, which posits that any monetary gain is better than no gain[7] and all offers should be accepted. Despite a breadth of studies describing decision outcomes in the UG[8-11], the value computations underlying human responder behaviour in iterative games remain elusive and summary statistics describing average acceptance probabilities at different offer amounts form the only primary outcome measure commonly reported in the literature.

A key factor which can also influence one's negotiation strategy in social interactive decision-making relates to negative or positive biases that distort the way people perceive others' emotions (e.g. thinking that the other person displayed a negative facial emotion when in fact s/he was neutral). During goal-driven social interactions (e.g. in various negotiation situations), others' facial emotions can provide us a window into how they perceive our requests, helping us to decipher their otherwise hidden valuation processes. Although humans are known to detect subtle changes in others' facial emotions, the existing literature also suggests that people are prone to affective biases in facial emotion recognition[12-14]. Only a few decision-making studies have investigated the effect of proposers' facial emotions on human responder behaviour in the UG. A previous study showed that responders are consistently more likely to accept offers coming from attractive faces of the opposite sex irrespective of the offer amount [15], while a large-scale online study suggested that offers coming

from proposers with smiling faces are more likely to be accepted relative to those coming from angry faces[16]. However, a key limitation of the previous studies is the experimental approach: pairing affective faces *randomly* with different monetary offer amounts in *one-shot games*. By this methodology, on each trial, participants are asked to respond to a stimulus which is intended to be completely *independent* of what they were presented with in the preceding trial(s). Considering that in daily social interactions people's facial emotions do not jump randomly from one affective state to another, the previous experimental approaches would only have limited ecological validity in terms of capturing real-world human social interactive decision-making processes. In order to improve on this key limitation, we designed a novel and *iterative* UG task in which proposers' facial emotions and offer amounts were generated from two sliding windows with transition probabilities based on participant responses in the preceding trials (Figure 1). We had previously argued that this approach would break the trial-wise independence of experimental stimuli, allowing participants to experience a gradually changing social interactive decision-making environment based on their responses in the previous trials[17]. These modifications to the UG allowed us to model key influences on participant choice behaviour during social interactive decision-making: the magnitude of social rewards and the proposer's affective states. Our *a priori* hypothesis was that the proposers' facial emotions, the offer amounts and an interaction between these domains should influence participant's decisions to accept/reject offers. In the following sections, by mathematical modelling of participant choice behaviour, we will describe how the proposer's facial expressions, which are perceived nonlinearly, influence human responders' value computations by acting selectively on perceived self—other inequality in the UG.

Figure 1. Experimental timeline of the novel Ultimatum Game task. On each trial the participant is presented with an affective face of the proposer/confederate (i.e. the red arrow) followed by the offer. In response to participant's decision (i.e. accept versus reject), the proposer's facial emotion may stay the same or change to a neighbouring stimuli based on predefined transition probabilities associated with each response type (e.g. the proposer is more likely to be happier if the offer is accepted). Similarly, based on other predefined transition probabilities, the offer on trial (t+1) may stay the same or may be revised to one of neighbouring offer amounts based on participant response (e.g. 200 offer as shown in the example above for trial (t) may increase and become 250 on trial (t+1), after participant rejected the 200 offer on trial (t)). The predefined transition probabilities for facial emotions and offer amounts for the novel UG task are available in Supplementary Materials.

Previous studies highlighted a role for the pupil-linked central arousal systems in human reinforcement-learning (RL) and value-based decision-making, particularly those performed in dynamically changing environments [18-20]. Recent neurophysiology studies demonstrated that changes in pupil size reflects the firing rate of the central norepinepheric neurons in the locus coeruleus[21,22] (LC). These studies provide a quantitative support for a number of converging theoretical [23] and experimental accounts of human behaviour [18-20,24], all implicating a role for the central norepinephrine (NE) system in guiding behavioural adaptations in response to environmental change, as assessed by measuring pupil size. Nevertheless, the role of pupil-linked central arousal systems during social interactive decision-making remains unknown. Considering that our experimental task was specifically tailored to allow participants to experience an evolving interpersonal negotiation environment, we asked healthy volunteers (N=44) to perform the novel UG task while undergoing pupillometry and investigated the role of pupil-linked central arousal systems in social interactive decision-making. Informed by previous studies, we expected pupil size

to encode a surprise response (e.g. offers and/or proposer's affective reactions), as well as showing sensitivity to the changes in the proposer's affective states. In line with these predictions, we present results highlighting the role of central arousal systems during social interactive decision-making, by showing that pupil size is sensitive to the proposer's affective reactions and encodes a model-based surprise response associated with offers which violate the participant's expectations from the proposer.

Results.

Participant Demographics. Forty four participants recruited from the general public completed the UG experiment with pupillometry. The demographic details of this cohort are summarised in Table 1.

Table 1. Demographic details of participants

Measure	Mean (SD)
Age	33.7 (11.30)
Gender	68.18% Female
QIDS-16	8.11 (7.60)
Trait-STAI	42.77 (13.52)
State-STAI	33.43 (12.21)

QIDS-16; Quick Inventory of Depressive Symptoms, 16 item self-report version. Trait/State-STAI; Speilberger State-Trait Anxiety Inventory. Note that scores of 6 or above on the QIDS-16 indicate the presence of mild depressive symptoms. The Trait/State-STAI has no standard cut-off scores.

Human participants prefer fair monetary splits. Participants initially rated 100 different Ultimatum offers presented in randomised order, on a 1-9 Likert scale indicating how much they would like the proposed offer (all offers between £0.50 and £9.50 expressed in pence). These ratings allowed us to develop liking-based decision models for the main social interactive experiment. The liking ratings monotonically increased from 50p to 500p (i.e. 50/50 split between proposer and responder) where they peaked. The liking ratings were lower for offers advantageous for the participant (>500p) relative to the 50/50 split, indicating inequality aversion (Supplementary Figure 1).

Nonlinearity in human facial emotion recognition. After rating the Ultimatum offers, participants rated their proposer's facial emotions, again on a 1-9 Likert scale (i.e. from negative to positive). Overall participants' Likert ratings correlated highly significantly with the emotional intensity of the proposers' facial expressions (average correlation coefficient r= .869, p<.001). However, participants were significantly better at accurately rating proposer's faces displaying positive emotions relative to negative emotions (average r values .821 versus .539, respectively;

t(86)=-4.55, p<.001). This indicated that participants' affective biases were more prominent for negative emotions (i.e. a larger deviation from the dashed diagonal line in Figure 2A). In order to capture participants' social affective biases, which we thought should influence value computations in the UG, we further analysed these ratings by exploiting the properties of a 2-parameter exponential-logarithmic function (see Materials and Methods, Eq.1). This novel analysis approach demonstrated that participants perceived their proposer's affective states nonlinearly, albeit with some individual variability (Figure 2A). We further investigated whether the parameter estimates from this model were influenced by participants' own mood states (i.e. factors such symptoms of depression and anxiety). This analysis suggested that none of the continuous or categorical variables that we considered in the regression model significantly influenced estimates of the model parameters (Figure 2B). Factors such as opponent type (i.e. whether the proposer was a confederate or a computerised opponent) or opponent sex did not influence the parameter estimates either, indicating that the nonlinearity captured in participants ratings was not a direct result of the potential nonlinearity in the way proposers might have expressed their emotions while their pictures were taken initially.

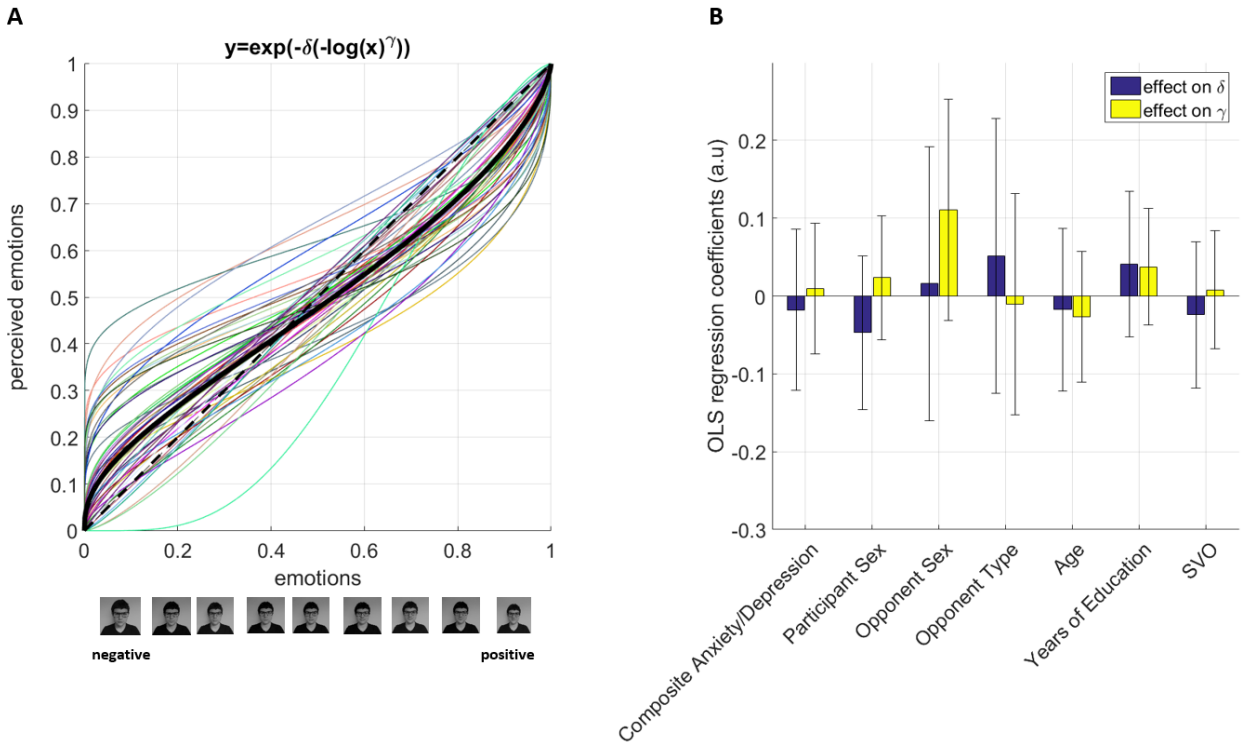


Figure 2. Results of the facial emotion rating task. (A). Participants perceived their opponent's facial emotions nonlinearly. The x-axis shows the proposer faces assembled from negative to neutral to positive (i.e. same as in Fig.1), and y-axis represents participants perceived emotions according to the best fitting nonlinear weighting model. Thick black line designates the population mean. **(B)** The model parameters [δ, γ, also see Eq.1] were not influenced by factors such as symptoms of depression and anxiety or participant and proposer sex. Composite depression and anxiety scores were established for each participant by linearly transforming (i.e. summing up scores from each domain within-subjects) the z-scores of depression, and state and trait anxiety measures to avoid collinearity in the model, as these measures were

highly correlated with each other in this cohort of non-clinical volunteers (all r(42)>.69, all p<.001). Opponent type designates whether participants were told they would be playing against a human confederate or a computerised proposer. SVO: Social Value Orientation, which is a continuous measure defining one's degree of prosociality. Error bars denote 95% CI.

Human choice behaviour violates the Rational Actor model. We first concatenated all participant data and binned average acceptance probabilities for all combinations of proposer's facial emotions and offer amounts (Figure 3A) and analysed this data with an ordinary least squares (OLS) regression model. This analysis suggested a main effect of facial emotion (based on t-tests on OLS coefficient estimates, t (43) =8.43), a main effect of offer amount (t (43) =8.85) and a significant facial emotion x offer amount interaction term (t (43) =3.70) influencing participants' probability of accepting an offer (all p<.001, Figure 3B). This means that people were more likely to accept unfair offers if the proposer's facial emotion was more positive, and outlines the extent of irrational economic decision-making in the UG. However, it is important to point out that these simple behavioural effects give a bird's eye view but cannot account for the iterative nature of social interactive decision-making (see results and modelling in the subsequent sections). For completeness, the average number of trials participants spent in each state-space during the UG experiment (facial emotion x offer amount) is shown in Supplementary Figure 2.

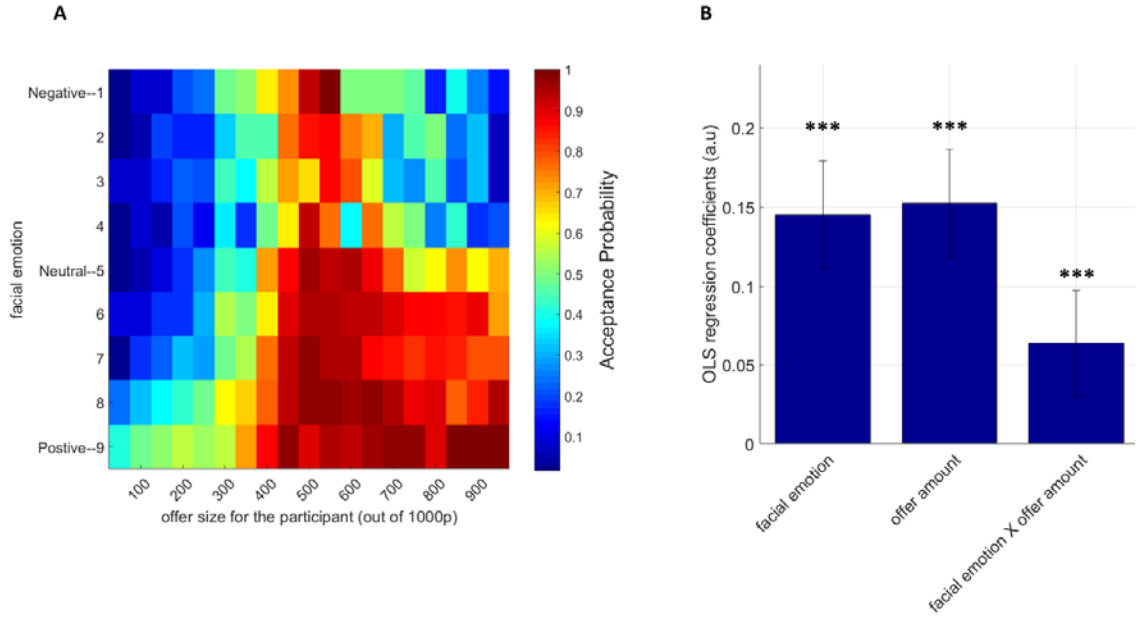


Figure 3. Behavioural results from the Ultimatum Game. (A). Participants' average acceptance probabilities across all possible combinations of proposer's facial emotion (y-axis) and offer amounts (x-axis) represented as a heat map. Colour bar shows the probability of accepting an offer. Changes in the colour gradient in the heat map suggests that unfair offers coming from positive faces were more likely to be accepted relative to offers associated with negative facial emotions, even if the offer amount is advantageous to the participant. **(B)** A formal OLS regression analysis conducted on the acceptance probabilities indicated a significant main effect of facial emotion, a main effect of offer amount and a significant facial emotion by offer amount interaction term influencing participants' probability of accepting an offer (***p<.001).

In iterative games recent history continue to influence participant choice behaviour. One of the main features of our experimental design was that participants responded to offers generated based on their responses in preceding trials. We used this approach to break the trialwise independence of stimuli commonly employed in previous studies. Consequently, we investigated how stimuli shown in preceding trials (i.e. n-1th to n-3th) as well as participants' previous decisions, influenced their choice behaviour on the current trial (i.e. the nth trial) using a logistic regression model. There were four regressors in this model: proposer's facial emotion, the offer amount, a facial emotion x offer amount interaction term and the participant choice. This analysis suggested all regressors from the n-1th trial significantly influenced participant choice behaviour on the current trial (all $|t(43)| > 2.84$, $p < .01$), with offer amount on the previous trial being the most significant influence ($t(43) = 9.56$, $p < .001$; Figure 4). The influence of these variables on participant choice behaviour decayed further down the trials. These results are also in line with the general notion that human choice behaviour in social interactive decision-making games can be defined in terms of n-1 (i.e. memory-1) conditional-probabilistic strategies[25].

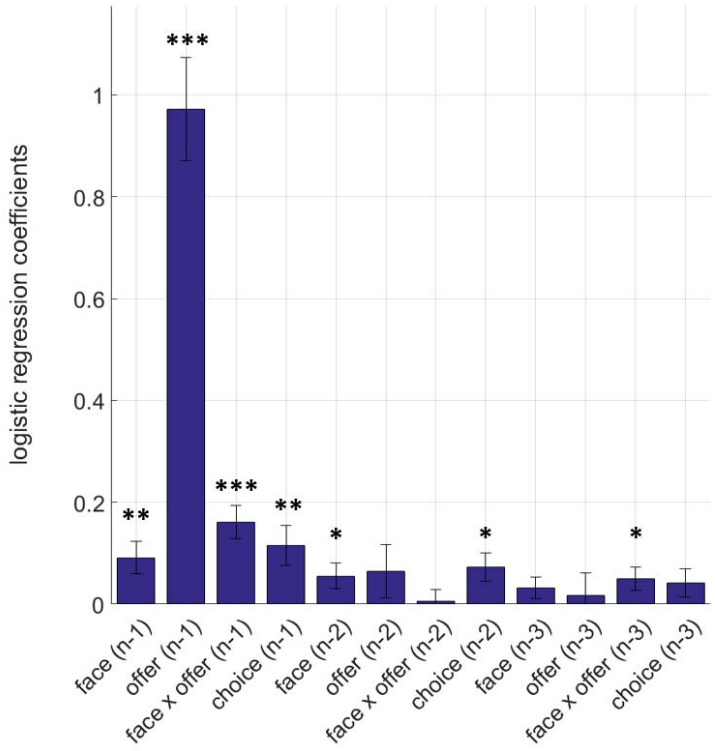


Figure 4. Logistic regression analysis of participant choice behaviour. Coefficient estimates from the logistic regression model fitted to participant choices on the current (nth) trial indicates that all regressors from the n-1th trial significantly influence participant choice behaviour (***p<.001, **p<.01). Absolute values of the coefficient estimates are shown for plotting purposes. The coefficient estimates for the influence of previous choices were all negative, indicating that offers on the current trial is more likely to be accepted if the offers on previous trials were rejected. The influence of these variables decayed down the trials. Error bars denote ±1SEM.

Proposer's affective responses dynamically modulate perceived self—other inequality. We fitted a number of computational models which we considered to describe participant choice behaviour in the iterative UG task (see Methods and Materials for model descriptions). The best-fitting model (Model 7), was able to predict participant choices in 83.3% of the trials, assumed that social affective biases which modulate how the proposer's facial emotions are perceived (as shown in Figure 2A), act on participants' perception of inequality[26] in the UG, and relaxes the negative valuations associated with it (Eqs. 1 and 9). In descriptive terms, this would mean that if the proposer insists on the same offer amount that is rejected iteratively by the participant, and continues to respond to the participant's rejections by displaying increasingly negative emotions, at some point the proposer can overcome the participant's negative valuation associated with perceived self—other inequality. This model can also flexibly adapt to other situations which occur during the game. For example, in situations where the proposer's facial expressions are neutral, the affective influence part of the model would nearly diminish (Eq. 9), allowing participants to hold on to their perceived inequality. In situations in which the proposer displays increasingly positive emotions in each iteration, the model then reduces the overall influence of perceived inequality on decision-values, accounting for compromises (e.g. "the offer is unfair, but if I accept it, at least it makes the other side seems to be happy"). Bayesian model selection metrics[27] supported these assertions, showing that the model in which facial emotion recognition biases selectively act on the inequality term (Model 7), but not on the self-reward amounts (Model 8), or both the self-reward and the inequality term independently (Model 9, Supplementary Figure 3) fits better to explain participant choice behaviour. The *parabolic* (Model 7), rather than an exponential (Model 6, Supplementary Figure 3), shape of this affective influence indicates that proposer's increasing negative or positive facial emotions act on the inequality term in a similar manner, while neutral facial emotions would have negligible influence on participant's perception of inequality. Further analysis of trials mispredicted by the best-fitting model did not show any significant main effect of the proposer's facial emotions or offer amounts (Supplementary Figure 4), indicating that the model does not fail systematically in converting these input stimuli into decision-values. However, there was a significant facial emotion x offer amount interaction in the mispredicted trials ($t(43)=-3.2452$, $p<.01$). Negative regression coefficients on this interaction term indicate that the model struggled to account for participant choice behaviour at the extremes (e.g. unfair offers coupled with very positive faces).

Similar to the OLS analysis that we reported for social affective bias parameters (Figure 2B), we analysed which variables influence the parameter estimates of the best-fitting choice model in the UG. This analysis suggested a significant relationship between participants' social value orientation

(SVO, as measured by the SVO Slider Measure[28]) and parameter estimates for the inequality term, meaning that people with higher SVO scores (i.e. people with more altruistic tendencies) perceive self—other inequality more negatively (t (43)= -2.166, p=0.036, Figure 5).

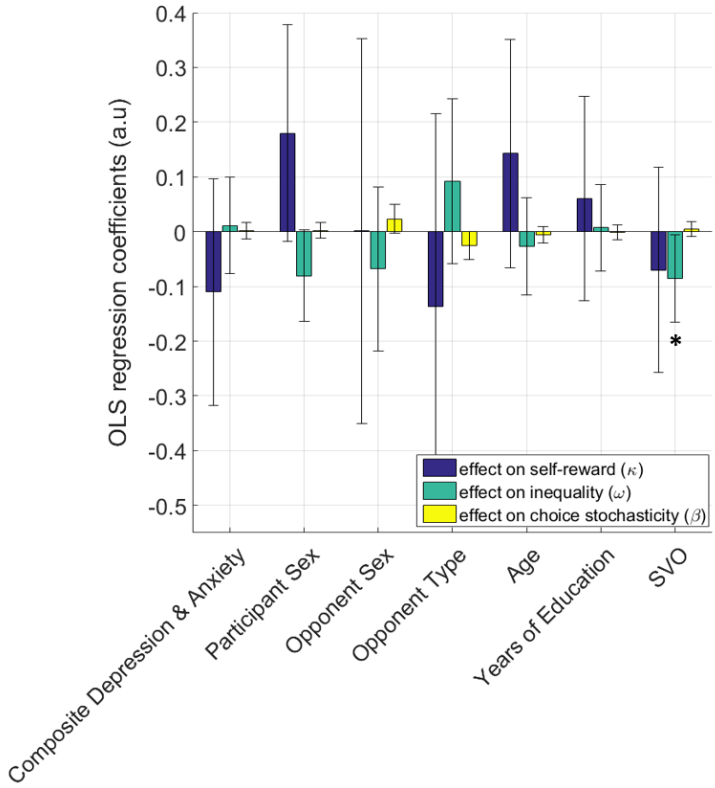


Figure 5. Prosocial individuals perceive self-other inequality more negatively in the UG. Coefficient estimates from an OLS regression model fitted to parameter estimates of the best-fitting computational choice model (i.e. Model 7) suggested that people with higher social value orientation will perceive self-other inequality more negatively (*p<.05). A generate-recover simulation analysis (50 iterations) based on stochastic choices generated by this model demonstrate the stability of the estimated parameters (Supplementary Figure 5). Error bars denote 95% CI.

Pupillometry Results. We analysed participants' pupil response during the decision stage of the UG task (i.e. the window from the presentation of the offer until the end of outcome presentation). A simple model-free analysis of pupil response done by binning average pupil size for all combinations of proposer's facial emotions and offer amounts (Supplementary Figure 6A), followed by an OLS regression analysis (i.e. comparable to model-free behavioural analysis reported in Figure 3B) suggested a significant main effect of the proposer's facial emotions on pupil size (t (42) =-2.22, p=0.028), i.e. pupil dilating more when the proposer is displaying negative facial emotions (Supplementary Figure 6B).

We further analysed the pupillary data with a complementary OLS model to investigate the degree to which regressors generated under the best-fitting computational model correlated with pupil size

294 during the UG experiment (see Materials and Methods for the details of the pupillary regression
295 model, Eq. 11). One possible caveat that we evaluated quantitatively before fitting the pupillary
296 regression model is the correlation between proposers' perceived facial emotions and the offer
297 amounts given to the participant. Normally, one would try to decorrelate these regressors as much
298 as possible to evaluate their unique pupillary or neural signatures. However, in the case of our task,
299 the computerised strategy was designed to display positive faces with higher probability if the offers
300 were accepted (as should logically happen in interpersonal exchanges in real life). In the extreme
301 case of a proposer's facial emotions and offers being completely decorrelated, the computerised
302 proposer would no longer be perceived as a human proposer (e.g. proposer reacting to participant's
303 decisions by showing random emotions or offers). The histograms of correlation coefficients
304 between social affective biases (i.e. proposer's facial emotions modulated by the nonlinear
305 weighting model, Eq.1) and decision-values generated under the best-fitting model for each
306 participant are shown in Supplementary Figure 7A (correlation coefficient *r* (mean±SD) =.058±.26). In
307 a similar manner to our previous study[3], we also asked our participants a number of questions
308 related to how they felt about their proposers to make sure that the computerised strategy was
309 perceived as "human-enough" (full set of questions given in Supplementary Figure 7B legends). On
310 average, participants were able to identify more than one person from their social circles who would
311 make offers and display affective reactions in a similar manner to the computerised proposer
312 (response to Q3; mean (±SD) =3.82(±.40); t (43) =7.12, p<.001), reassuring that our experimental
313 manipulation was successful in terms of the computerised proposer adequately mimicking human
314 behaviour while keeping the correlations between perceived faces and offer amounts within an
315 acceptable range.

316 **Pupil size encodes the opponent's affective responses which dynamically modulate**
317 **perceived self—other inequality.** Two key regressors that we were interested in were the
318 decision-values generated by the best-fitting model and proposers' facial emotions modulated by
319 the nonlinear weighting function. Time evolution of estimated coefficients for these two regressors
320 are reported in Figure 6. Subsequent analysis (i.e. average regression coefficients binned at each
321 second after offer presentation, analysed by 1-sample t-tests from baseline) indicated that pupils
322 dilate more in reaction to proposer's faces perceived as displaying negative emotions (peak response
323 between 1000-2000 ms, t (42)=-3.638, p=.001, Figure 6B). This result is in agreement with the
324 model-free pupil results reported in the preceding section, and indicates that the proposer's
325 affective responses to participant decisions, which dynamically modulate self—other inequality in
326 the best-fitting computational model, is encoded by the pupil-linked central arousal systems.

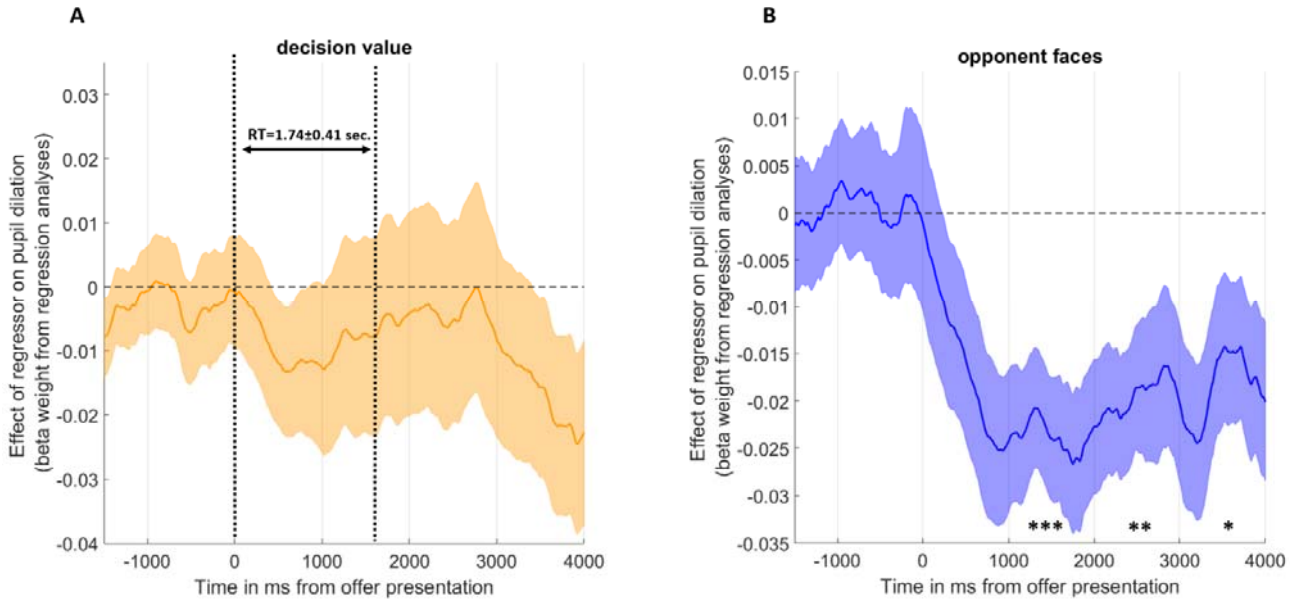


Figure 6. Pupillary signal of decision-values and social affective biases. (A) Coefficient estimates from the pupillary OLS regression model correlating with decision-values (i.e. the orange line and shading ±1SEM) from the best-fitting behavioural model. Although time evolution of regression coefficients dip during offer presentation (the window marked with dashed lines designating the decision reaction time (RT)) and post-decision interval, indicating that pupil dilate more to lower value offers, this signal was not statistically significant. **(B)** The proposer's faces perceived as negative will lead to pupil dilation (i.e. the blue line and shading ±1SEM). The signal is statistically significant and remains significant from ~1 second after outcome presentation (***p<.001, **p<.01,*p<.05). Error shading denotes ±1SEM.

The other regressors that we were interested in while constructing the pupil model were those quantitatively defining how the social interactive decision-making environment changed (i.e. environmental volatility and environmental noise[29]), as well as participants' response to those changes (i.e. surprise). These were estimated from the raw stimuli (i.e. the offer amounts and facial emotion valence on each trial) by a recursive Bayesian filter[29] that can estimate the generative statistics of the stimuli uniquely for each participant, and helps with objectively quantifying how the social interaction environments changed, as these changes also depended on participant choice behaviour, meaning that each participant experienced a unique sequence of stimuli. The analyses of these regressors indicated that pupils dilate more in response to surprising offers ($t(42) = 2.166$, $p = .036$, Figure 7A). Regressors defining environmental volatility and noise did not lead to any statistically significant pupil response, suggesting that pupil size does not encode higher order statistics of the social interactive decision-making environment.

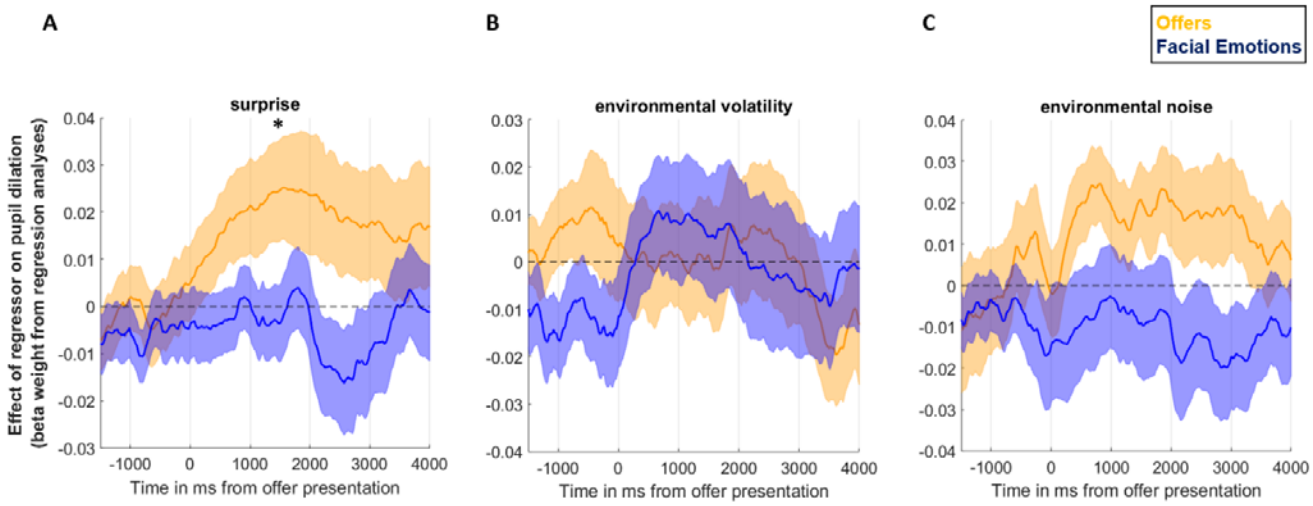


Figure 7. Pupillary signal correlating with regressors extracted by the Bayesian filter. (A) Time evolution of coefficient estimates from the pupillary OLS regression model correlating with surprise associated with offer amounts and proposer's facial emotions. The surprise signal peaked around decision RT (*p<.05). **(B-C)** Time evolution of regression coefficients from the pupillary regression model for regressors describing environmental change. Pupil response was not statistically significant for any of these regressors. Error shading denotes ±1SEM.

Surprising offers which violate participants' expectations are less likely to be accepted. At the last step we investigated the degree to which regressors describing the changes in the social interactive decision-making environment which were computed by the recursive Bayesian filter also influenced participant choice behaviour. We fitted a logistic regression model to participant choices in which surprise, volatility and noise regressors were predictive variables (for both the proposer's facial emotions and the offers). We further included the factors which we had an already established influence on choice behaviour (i.e. facial emotions, offer amount and their interaction as reported in Figure 3B) and the trial number (i.e. 1 to 240, total number of trials) as regressors of no interest. After excluding six extreme outliers, this analysis indicated that surprising offers were less likely to be accepted (all $t(37)=-2.469$, all $p=.018$), whereas noisy fluctuations in the proposer's facial emotions increased participant's probability of accepting an offer ($t(37)=2.024$, $p=.05$, Figure 8). Taken together, surprise response to offer amounts seems to be the overarching process which correlate with pupil size (Figure 7A) and influence participant choice behaviour. A final control analysis investigating the correlation between the surprise regressor generated uniquely for each participant and the offer amounts observed by the participant suggested a marginally positive correlation in this cohort (correlation coefficient $r(238) = .17\pm.09$ (i.e. mean±SD), Supplementary Figure 8). This indicates that offers which violated the expectations of the participant, but not necessarily the lower offers, were less likely to be accepted.

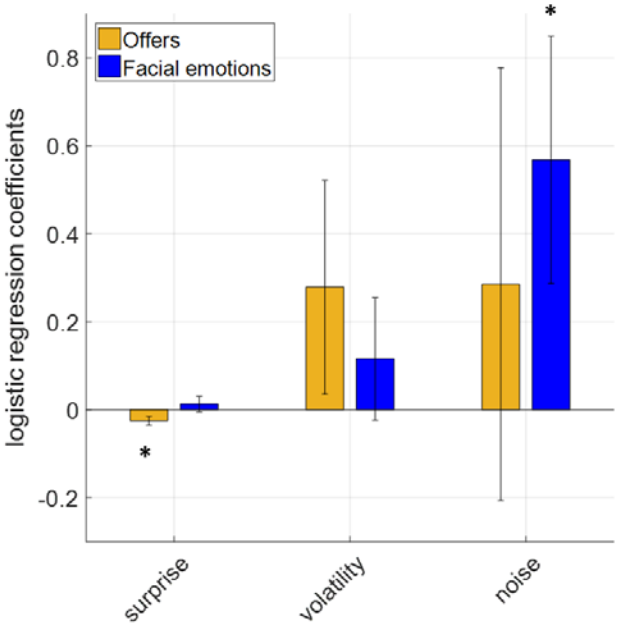


Figure 8. Influence of regressors extracted by the Bayesian filter on participant choice behaviour. Significantly negative correlation coefficients were observed only for the way offer amounts changed during social interactive decision-making. The results suggest that offers associated with greater surprise, environmental volatility and noise are less likely to be accepted (***p<.001, **p<.01). Error bars denote ±1SEM.

Discussion

In the present work we describe value computations underlying human responder behaviour in an iterative UG task which also involved participants observing the proposers' affective reactions. The results that we present here indicate that human participants exhibit perceptual social affective biases which are represented nonlinearly (Fig. 2A). We show that proposers' facial emotions significantly influence participant choice behaviour in social interactive decision-making (Fig. 3A-B). The influence of the proposer's facial emotions on participant choice behaviour is also shown in results from different methods of analysing the behavioural data (i.e. both logistic regression and computational model-based). Reassuringly, we show that parameter estimates for the inequality term from the best-fitting computational model were significantly negatively correlated with participants' social value orientation (SVO), capturing the intuition that people with higher prosocial tendencies perceived self—other inequality more negatively, and were less likely to accept unfair offers (Fig. 5). Computational modelling of participant choices further revealed that social affective biases dynamically modulate participants' perception of inequality, relaxing its negative influence in a *parabolic* shape (i.e. Model 7). This meant that participants were more likely to accept unfair offers, irrespective of whether they were advantageous or disadvantageous, when their rejections are persistently confronted with an affective response (i.e. all emotional faces apart from a neutral facial expression) coming from the proposer (also partially illustrated in the model-free faces x offer amount interaction effect, Figure 3). This model demonstrates that human inequality aversion is a malleable cognitive process, and can flexibly account for human behaviour in a number of social interactive decision scenarios, for example rise of compromise behaviours in interpersonal negotiations under affective load. The pupillary regression analysis shows that proposers' affective responses are tracked by corresponding changes in participants' pupil size (Fig. 6B), while a surprise response estimated by a recursive Bayesian filter in response to offers given by the proposer led to pupil dilation (Fig. 7A). This indicates that pupil size also encodes violations of participants' expectations. Subsequent analysis suggests that this surprise response is another overarching variable which is encoded by the changes in pupil size and also influence participant choice behaviour (Fig. 8). Thus, our data suggests that unexpected offers lead to pupil dilation and are less likely to be accepted. To the best of our knowledge, these results constitute the first line of evidence giving a detailed account of (i) how opponent's affective responses influence value computations in social interactive decision-making; and (ii) the role of the pupil-linked central arousal systems in these value computations.

Among behavioural economic games, the UG is one of the most commonly used zero-sum game, meaning that gains are mutually exclusive between the proposer and the responder. The

426 linear payoff structure and sequential decision-making nature of the UG makes it a good candidate
427 for computational modelling compared to other nonzero-sum games like the Prisoner's Dilemma
428 (PD). The UG is known to have a strong non-monotonicity, which indicates that people's acceptance
429 probability does not increase monotonically with increasing self-reward magnitudes[30]. We
430 demonstrated that our participants also behaved in this manner, as indicated by results from the
431 analysis of choice behaviour (Figure 3A), and liking ratings (Supplementary Figure 1). This non-
432 linearity in acceptance probabilities is more likely to be driven by inequality aversion (Eq. 6, ω
433 parameter). Rejection of unfair offers driven by perceived inequality contradicts the Rational Actor
434 Model, which is regarded as the optimal decision-making policy in the UG from an economic point of
435 view, and dictates that accepting all offers, irrespective of inequality, maximises the reward rate.
436 Within this framework, and by using a confederate design, we demonstrate that a modified UG task
437 can adequately mimic social interactive decision-making in an ecologically valid manner, as
438 supported by responses from participants on the behaviour of the computerised opponent
439 (Supplementary Figure 7B). Our results demonstrate that the affective content of the proposers'
440 facial expressions serve as another source of *suboptimality* in social interactive decision-making. This
441 finding which we demonstrate both in our model-free (Figure 3) and model-based analyses,
442 contradicts with the predictions of the Rational Actor model, which would posit that a strategy
443 ignoring the opponent's affective states would be optimal.

444 The present results complement the findings of a recent work in which we described a
445 computational model accounting for human *proposer* behaviour in the UG[3]. In these two studies,
446 focussing on value computations underlying the proposer's and the responder's behaviour
447 separately allow us to restrict the vast model space and identify suitable models accounting for
448 human social interactive decision-making. Future studies should go one step further than these
449 preliminary reference points that we identified in the UG decision model space, and independently
450 validate risky decision-making models accounting for proposer behaviour versus inequality aversion
451 models accounting for responder behaviour in a two-person interactive experimental design. The
452 extent of the decision model space has been one of the key challenges which limited the number
453 studies reporting computational models of choice behaviour in social interactive games[31-33], as the
454 difficulty associated with modelling recursive ToM processes is making social interactive decision-
455 making a topic "too hot to handle". Although a recent neurophysiology study in monkeys has shown
456 that it is possible by-pass some of these difficulties by modelling the proposer's future decisions in a
457 binary format (i.e. cooperate versus defect in PD) to illustrate underlying neural correlates of ToM
458 processes[34], these novel approaches require neural data with very high temporal precision which has
459 not yet been implemented in human participants. As a result, and despite the fact that humans are

460 social animals, our understanding of social interactive decision-making processes in healthy and
461 patient groups are lagging far behind other well-defined cognitive processes such as reinforcement
462 learning (RL)[19,20,35,36].

463 A number of previous studies reporting computational mechanisms underlying learning and
464 decision-making in dynamically changing environments interpreted phasic changes in pupil size as an
465 index for the firing of the central NE neurons[18-21]. In the current work, we showed that pupil dilation
466 correlates significantly (i) positively with surprise associated with offers (Fig. 7A), and (ii) negatively
467 with proposers' affective reactions (Fig. 6B). Although previous work suggested that norepinephrine
468 reuptake inhibitors (SNRIs) modulate neural responses to facial emotions[37], indicating a role for the
469 central norepinephrine system in facial emotion recognition, it is important to acknowledge that
470 pupil dilation in response to task components may also be under the influence of cholinergic activity
471 in the brain (see a more detailed discussion in Faber, 2017[38] and Muller et al., 2019[24]). Another key
472 neurotransmitter which is involved in social decision-making[5,11,39] and facial emotion recognition[14,40-
473 42] is serotonin (5-HT), and previous work has shown that pharmacological agents acting on the 5-HT
474 system also modulates pupil dilation[43,44]. Teasing out the influence of these neurotransmitters on
475 pupil dilation during social interactive decision-making ideally requires experimental pharmacology
476 methods and should be tested in future studies to further understand mechanisms of causality. The
477 current experimental approach could also be useful in teasing apart neural responses associated
478 with information processing during social interactive decision-making, considering existing literature
479 clearly demonstrates that facial emotion recognition and social decision-making activate fronto-
480 striatal and limbic regions[6,8,33,39,45-47]. The main strength of the current experimental design is that it
481 probes facial emotion processing and social decision-making domains simultaneously with a
482 relatively fine gradient (by generating stimuli probabilistically from two sliding windows, 9 different
483 facial emotions x 19 different offer amounts, in total 171 unique stimulus combinations, Fig. 2A),
484 therefore it can be used as an experimental probe for addressing these mechanistic questions about
485 information processing during social decision-making.

486 One of the key rating tasks which also informed our modelling of participant choice
487 behaviour in the UG evaluated participants' social affective biases to proposers' facial emotions. We
488 modelled participants' ratings on a Likert scale by exploiting the properties of a 2-parameter
489 weighting function. Although our modelling approach revealed individual variability in these
490 perceptual biases, the parameters of this model did not correlate significantly with symptoms of
491 depression (QIDS range: 0-27) and anxiety in this non-clinical cohort (Figure 2). These results are not
492 in line with predictions based on some of the previous studies in depressed groups which used the
493 FERT[12,13]. Consequently, it may be worthwhile to highlight some of the experimental differences

494 between the traditional FERT and the facial emotion rating task that we used in the current study. In
495 the traditional FERT, participants are presented with affective faces for a very brief period,
496 approximately for 800 milliseconds; and they are asked to label faces into one of seven different
497 emotional categories: sad, angry, happy, surprise, fear, disgust and neutral. Brief stimulus
498 presentation duration does not allow too much time for participants to decode the individual parts
499 of the face while forming a judgment about its affective content. The faces are presented in an oval
500 frame cutting out some of the facial features such as hair and ears (approximate size 56.25 cm^2). It is
501 possible that these aspects of the FERT create ambiguity and an information gap which probes
502 affective biases more strongly in clinical groups relative to non-clinical volunteers. On the other
503 hand, our rating task was self-paced (i.e. ratings were made while viewing the faces, RT (mean ± SD)
504 = 2.90 ± 1.04 seconds). It is possible that accurately rating affective faces on a scale may be more
505 challenging than categorising them into predetermined labels (e.g. happy, sad, fear etc.). In the
506 rating task, the faces were presented in a rectangular frame similar to a passport picture occupying a
507 102.7 cm^2 area. These modifications allow participants to gather more information about the
508 affective content of the faces, reducing ambiguity and increasing ecological validity of the stimuli
509 and the ratings (e.g. the fact that in real life social interactions people have reasonably long time to
510 observe others' facial emotions, see Sonkusare, Breakspear and Guo (2019) for a critical appraisal of
511 existing task designs in cognitive neuroscience[48]). Therefore, in future studies, it would be very
512 important to gather large-scale data to validate the affective content of the facial expressions used
513 in the current study, which can help understanding how symptoms of depression and anxiety
514 influence facial emotion recognition in the wider population. While our current modelling results
515 suggest that facial emotion processing (i.e. evaluating intensity and valence) and social interactive
516 decision-making processes are not systematically impaired by increasing symptoms of depression
517 and anxiety in a group of *non-clinical* volunteers, it would be informative to implement the current
518 experimental design in clinical groups, such as patients with major depression, in which facial
519 emotion recognition and social decision-making processes were shown to be affected in previous
520 studies [9,17,49,50].

521 Taken together, our key results demonstrate that, under affective load, inequality aversion
522 in human participants is a malleable cognitive process. We showcase that central arousal systems
523 (i.e. reflected in pupil size) are involved in value computations during social interactive decision-
524 making and track the opponent's affective responses which dynamically modulate perceived
525 inequality. These findings may have important implications for understanding the cognitive
526 processes that underlie suboptimal outcomes (e.g. compromise behaviours and settling down for an
527 unfair split in interpersonal negotiations) in social interactive decision-making.

528 **Methods and Materials.**

529 **Participants.** Forty four participants were recruited from the local community via advertisements.
530 Potential participants who had a history of neurological disorders or who were currently on a
531 psychotropic medication were excluded from the study. In order to increase the overall
532 generalisability of study results, eleven confederates were recruited from the staff of University of
533 Oxford Department of Psychiatry. The confederates attended to two testing sessions. In their first
534 visit, they were instructed to display different emotions (i.e. 9 different from negative to neutral to
535 positive) while the pictures of their faces were taken. These pictures were later used in the facial
536 emotion rating task and the Ultimatum Game (UG, Fig. 1).

537 **Procedures.** Before the experimental tasks, participants completed the Spielberger State-Trait
538 Anxiety Inventory, Quick Inventory of Depressive Symptoms and Social Value Orientation (SVO)
539 Slider Measure [28] in a pen and paper questionnaire format. After these, participants completed two
540 rating tasks in which they were asked to rate various (i.e. in total 100 unfair, fair and advantageous
541 offers) Ultimatum offers coming from an anonymous proposer on a 1-9 Likert scale (dislike vs liking).
542 All offers involved splitting £10 between the proposer and the participant, and the offer amounts
543 were presented in pence unit. After that participants rated their proposers' (i.e. the confederate's)
544 pictures displaying different facial emotions, on a 1-9 Likert scale (i.e. from negative to neutral to
545 positive, 9 different emotions in 6 randomised iterations, a total of 54 ratings). These rating tasks
546 were administered to establish participants' baseline preferences independently, and the ratings
547 were later used to construct computational models accounting for decision-making processes in the
548 UG.

549 After the rating tasks, participants completed the UG while undergoing pupillometry recording
550 (n=44). The task consisted of 6 blocks of 40 trials each. Where available, each participant was paired
551 with one of 11 different confederates. The participants were told that they would be playing an
552 interpersonal negotiation game against another participant recruited from general public, and in the
553 game they would be interacting with the other person through internet connection to an online
554 server. To strengthen the confederate manipulation, the participants were told that their proposers
555 attended on 2 occasions, and in their first visit they also respond to the same questionnaires as the
556 participant did, and their pictures were taken while displaying different emotions, later to be used in
557 the negotiation game. For some participants (47.7%) it was not possible to arrange a confederate
558 due to feasibility issues (e.g. a mismatch between the participant, testing room and confederate
559 availability). Those individuals were explicitly told that they would be playing against a computerised
560 strategy which was developed based on the behaviour of a previous participant. We used this

561 manipulation in our previous work to investigate proposer behaviour in the UG[51]. In fact, all
562 participants played against the same computerised strategy which was developed to sample offers
563 and facial emotions probabilistically from two independent sliding windows.

564 In descriptive terms, the proposer strategy was designed to test the participants' acceptance
565 threshold by sampling offers probabilistically around the threshold (e.g. previously rejected offers
566 can stay the same mimicking an insisting behaviour, improve or even get lower), and displays
567 negative facial emotions with relatively higher probability when the offers are rejected or displays
568 positive facial emotions with relatively higher probability when the offers are accepted (details of
569 the computer strategy is available in Supplementary Materials.). A full debriefing letter summarising
570 the aims and objectives of the study along with reasons for deception was provided at the end of the
571 study.

572 At the beginning of the UG experiment, the participants were explicitly told that their proposers
573 would be selecting one offer out of a window of different offers to make a proposal. Participants
574 were told that this is to make sure that their proposers could not consistently make unfair or fair (i.e.
575 50/50 split) offers in which case the negotiation would get stuck in a limited range of offers. This
576 measure was taken to make sure that the decision-making process was confined to responding to
577 combinations of faces/offers in a gradually evolving task environment, and the influence of higher
578 order cognitive processes (e.g. Theory of Mind tracking[32], learning about the proposer's strategy) is
579 limited and/or becomes redundant. We think that UG is a particularly suitable task for this purpose
580 as it allows reducing model complexity (e.g. eliminating recursive models), relative to other tasks
581 such as the Stag Hunt[33], the Trust[52] or the Inspection games[31]. This is because the Rational Actor
582 model[7], which posits that any gain is better than no gain and all offers should be accepted, describes
583 the optimal strategy for maximising rewards. Secondly, recursive ToM models with which
584 participants can try to influence the proposer behaviour would only work effectively if the
585 proposer's subsequent offer is more than twice as good as the offer rejected on the current trial, as
586 otherwise the reward rate per trial cannot exceed the reward rate per trial if all offers are accepted.
587 However, we minimised this possibility in our task design (~9% of trials, offer amount (mean±SD):
588 132.6 ± 38), as offers were drawn from a sliding window and did not increase in a multiplicative
589 manner.

590 Just like in any traditional UG experiment, participants were told that their task is to accept or reject
591 these offers coming from the proposer. The participants were told that the accepted offers will be
592 distributed as proposed, but if they reject an offer both sides would get nothing for that trial. The
593 participants were told that after their decision, the proposer would see 9 faces displaying different

emotions (i.e. the same 9 faces the participant rated previously) and would select one to communicate how s/he feels in response to the participant's response and in the next trial the proposer would see another set of options, also giving him/her an opportunity to revise his/her offer. The participants were told that each block would start with a neutral face and a fair offer (i.e. 50/50 split) and can go any direction from that point onwards based on their negotiation ability. The participants were instructed that at the end of the game a computer algorithm would randomly select 20 trials and the outcome of those trials would be paid to each side. At this point we told participants that they may be inclined to accept all offers (i.e. the optimal decision-making according to Rational Actor model which posits that any gain is better than zero) so that those randomly selected 20 trials would always have a monetary outcome for the participant, but in that case, we told them, that their proposer may detect this tendency and try to make offers as low as possible. We then told participants to use the accept/reject responses strategically to negotiate better terms for themselves.

During pupillometry recording, participants' heads were stabilised using a head-and-chin rest placed 70 cm from the screen on which an eye tracking system was mounted (Eyelink 1000 Plus; SR Research). The eye tracking device was configured to record the coordinates of both of the eyes and pupil area at a rate of 500 Hz. The pupillometry data collection lasted approximately 70 min per participant.

Modelling affective biases in facial emotion recognition. We modelled participant rating responses to affective faces (on a 1-9 Likert scale from negative to positive) by exploiting the properties of the 2-parameter probability weighting function[53]:

$$\varepsilon = e^{(-\delta(-\ln(\varphi))^{\gamma})} \tag{1}$$

where φ is the true emotional state of the proposer's face as displayed, and can take values from 0.1 to 0.9. The parameters [δ , γ] determine the curvature of the weighting function and where it crossed the $\varepsilon = \varphi$ diagonal line (Figure 2A). We implemented the probability weighting function like a nonlinear regression model that minimises the difference between model estimates and participant's ratings (after performing a simple linear transformation by dividing the Likert ratings by 10, such that both the ratings and the estimates are bounded by 0 and 1).

Modelling liking ratings for Ultimatum Offers. In line with previous literature[45], we modelled participants liking ratings (χ) for each Ultimatum Offer (again, based on participant ratings on a 1-9 Likert scale) with a multiple linear regression model.

625 $$\chi = \phi_0 + \phi_1 R_S + \phi_2 |R_S - R_O| \quad (2)$$

626 where R_S is the self-reward and R_O is the reward amount to the proposer, and absolute value
627 difference accounts for how much the participant cares for inequality. Here, it is important to clarify
628 that because all offers involve splitting £10, R_O is not entered to this regression model as an
629 independent regressor as all monetary information is conveyed by the self-reward amount and the
630 inequality term.

631 **Modelling participant choice behaviour in the Ultimatum Game.** The model-free analyses of
632 participant choice behaviour indicated that both offer amount and the proposer's facial emotions
633 should influence how people generate decision-values in the UG. Here, we formally describe all the
634 models that we considered, to identify the cognitive model which accounts for participant choice
635 behaviour the best.

636 The first model that we considered assumes that participants construct the decision-value ($\tilde{v}$) of
637 each offer utilising a Constant Elasticity of Substitution (CES) function, commonly used to account for
638 consumer behaviour [54,55]. According to the CES function, the decision-value is computed as:

639 $$\tilde{v} = (\alpha R_S^{\rho} + (1-\alpha)|R_S - R_O|^{\rho})^{1/\rho} \quad (3)$$

640 where ρ is a nonlinear power utility parameter determining the concavity of preferences and α
641 determines how much weight is assigned for the self-reward magnitude or the absolute value
642 difference between the self and the other's reward magnitude (i.e. the inequality term).

643 We considered another model in which the decision-value is generated by comparing the inequality
644 term relative to one's fairness threshold:

645 $$\tilde{v} = \lambda - |R_S - R_O| \quad (4)$$

646 where λ is the fairness threshold parameter freely estimated between 50 and 950 (i.e. bounded by
647 the minimum and maximum offer amount), defining the participant's subjective threshold in term of
648 what they regard as acceptable.

649 The next model assumed that participants accept or reject offers based on their liking ratings, as
650 established by the independent rating task participants completed prior to the social interactive
651 decision-making task. In this model, participant's liking of offers during the UG is estimated by
652 feeding each participant's estimated coefficients from the linear regression model back to Eq.2.
653 Here, the decision-value is equal to:

654 $$\tilde{v} = \chi \quad (5)$$

655 We also considered another model with a similar structure in which the decision-values are
656 generated online during the social decision-making task, instead of depending on participant's
657 previous liking ratings. This model addresses the prediction that there will be a dissociation between
658 how much people like offers when these ratings do not have any financial consequence and how
659 they value them in a social interactive context with monetary consequences (i.e. the fact that
660 participants would be paid the outcome of 20 randomly selected trials). Here, the decision-value is
661 computed as

662 $$\tilde{v} = \kappa R_S - \omega | R_S - R_O | \quad (6)$$

663 For model simplicity we used a single inequality aversion parameter, instead modelling
664 advantageous and disadvantageous inequality separately. All models assume that conditions with
665 relatively higher subjective value should be more likely to be accepted and participants' acceptance
666 probability is generated by a sigmoid function:

667 $$q_A = 1/(1 + e^{-\beta \tilde{v}}) \quad (7)$$

668 where β is the inverse temperature term which modulates the stochasticity of participant choices.

669 We first chose between these models which define participants' likelihood of accepting an offer
670 solely based on the numerical components of the offer amount. We implemented this reduction in
671 model space based on our model-free analysis which suggested that offer amount has a greater
672 influence on acceptance probabilities than the proposer's facial emotions. Group-wise sum of
673 Bayesian Information Criterion (BIC) scores indicated that the model described by Eqs. 6 and 7 was
674 the best fitting model to account for how offer amounts were translated to decision-values.

675 We then used this best fitting model from the first stage as a template to further evaluate how facial
676 emotions of the proposers may influence the way decision-values are computed in the social
677 decision-making task. Based-on previous literature, we considered a model in which the effect of
678 proposer's facial emotion depends on the participants' individual variability in how malleable they
679 are to external emotional influence [56]:

680 $$\tilde{v} = \kappa^{(\varepsilon - \mu)} R_S - (\omega^{(\varepsilon - \mu)} | R_S - R_O |) \quad (8)$$

where parameters κ and ω are estimated between 0 and 10 and determines the degree to which the modulations of self-reward and the inequality term are subjected to emotional influence. In this model, social affective biases (Eq.1) act like an exponential function modulating this influence parameter [6] and μ is the value where perceptual biases crossover the diagonal line (Figure 2A, μ=0.4). We considered 3 variants of this model where proposer's facial emotions influence the self-reward amount (R_S) or the inequality term ($|R_S - R_O|$), or both independently.

We also investigated whether the proposer's facial emotions influence the inequality term in a parabolic, rather than an exponential functional form:

$$\tilde{v} = \kappa R_S + (\omega + (\varepsilon - \mu)^2) \, | R_S - R_O | \tag{9}$$

For any given offer amount, this formulation relaxes the negative modulation of inequality as the proposer's facial emotions are gradually getting negative or positive, while assuming that neutral faces would have limited influence on the inequality term.

Finally, we considered a competing model which assumes that the proposer's facial emotions influence the value of offers through a weighted integration.

$$\tilde{v} = w\tilde{v} + (1-w)(\varepsilon - \mu) \tag{10}$$

Here, *w* is a free parameter estimated between 0 and 1, and determines the degree to which the participant assigns credit to subjective value of the offers and/or to the proposer's facial emotions which are nonlinearly modulated by affective biases. The additive integration means that other's facial emotions should have an intrinsic value, an assumption that is in line with existing literature [57].

All model parameters were estimated by a Bayesian model fitting procedure, by calculating the full joint posterior distribution of the parameters over the whole parameter space, and deriving exact parameter values by integrating these probabilities with their corresponding discrete parameter values.

Pupillometry data preprocessing. Eye blinks were identified using the built in filter of the Eyelink system and were then removed from the data. A linear interpolation was implemented for all missing data points (including blinks). The resulting trace was subjected to a low pass Butterworth filter (cut-off of 3.75 Hz) and then z transformed across the session (Browning et al., 2015; Nassar et al., 2012). The pupil response was extracted from each trial, using a time window based on the presentation of the offer amount. This included a 7.5 second baseline period before the presentation of the outcome (including the period at the beginning of a trial marked by a fixation

cross and presentation of the proposer faces alone, Figure 1), and a 4.5 second period following offer presentation. Baseline correction was performed by subtracting the mean pupil size during the 7.5 seconds baseline period prior to the presentation of each offer, from each time point in the decision and outcome period. Individual trials were excluded from the pupillometry analysis if more than 50% of the data from the outcome period had been interpolated (mean =10.9% of trials) (Browning et al., 2015). The preprocessing resulted in a single sets of pupil timeseries per participant containing pupil dilation data for each of the included trials.

Regression analysis of pupillometry data. We implemented an OLS model in a similar manner to a functional neuroimaging (fMRI) analysis, by fitting the regression model to the pre-processed pupillary data at every 2-millisecond time point. The pupil model had 10 regressors as defined by the following linear regression equation:

$$\begin{aligned} pupil(2\pi r) &= \phi_0 + \phi_1 i + \phi_2 \tilde{v}^i_{Model7} + \phi_3 \varepsilon^i + \phi_4 surprise^i_{offer} + \phi_5 surprise^i_{faces} + \\ &\phi_6 vol^i_{offer} + \phi_7 vol^i_{faces} + \phi_8 noise^i_{offer} + \phi_9 noise^i_{faces} \end{aligned} \tag{11}$$

Here we provide brief descriptions for each regressor in the model. The regressor for the constant term (ϕ_0) captures the variance in pupil size across all trials in the task. The regressor (ϕ_1) accounts for the effect of trial numbers, as a proxy for accumulated fatigue (*i*: taking values from 1 to 240). We entered one regressor (ϕ_2) which represents the subjective value of each offer under the best-fitting behavioural model. The regressor (ϕ_3) encodes the perceived facial emotions modulated by 2 weighting parameters (Eq.1). The rest of the regressors were defined by a recursive Bayesian filter that we recently reported[27] which can optimally track the hidden structures (i.e. environmental volatility (i.e. vol in the above formula) and noisy fluctuations (i.e. noise) in the environment) of dynamically changing environments. The surprise regressor was congruent to the conditional –log probability of an offer coming from a distribution with mean and standard deviation (SD) estimated by the Bayesian filter. This would mean that stimuli which violate the expectations of the observer should lead to a greater pupillary surprise signal. This regressor was calculated for both the offers and the proposer's facial emotions.

ACKNOWLEDGEMENTS

This study was funded by National Institutes of Health Research (NIHR) Oxford Biomedical Research Centre funding allocated to EP. DAJM and EP collected the data. EP analysed the data. All authors contributed to writing up of the manuscript. The authors would like to thank Dr. Alexander Kaltenboeck for his help with the study. The views expressed in the manuscript are those of the authors and not necessarily those of the NHS, the NIHR or the Department of Health. MB is supported by a Clinician Scientist Fellowship from the MRC (MR/N008103/1) and by the NIHR Oxford Health Biomedical Research Centre. He has received travel expenses from Lundbeck for attending conferences and acted as a consultant for Jansen Research and CHDR. CJH has received consultancy fees from p1vital. Lundbeck, Pfizer, Sage Pharmaceuticals, Servier, Zogenixs and J&J.

References

1 Woodcock, A. & Stone, J. Brexit: Boris Johnson to give EU 'take it or leave it' ultimatum after Irish outrage at border plan. (2019, October 2).

2 Stone, J. EU gives Boris Johnson ultimatum: Show us Brexit plan in 12 days or 'it's over'. (2019 September 18).

3 Pulcu, E. & Haruno, M. Value Computations Underlying Human Proposer Behavior in the Ultimatum Game. *Journal of Experimental Psychology: General*.

4 Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 3531-3535, doi:10.1073/pnas.0630443100 (2003).

5 Crockett, M. J., Clark, L., Tabibnia, G., Lieberman, M. D. & Robbins, T. W. Serotonin Modulates Behavioral Reactions to Unfairness. *Science* **320**, 1739, doi:10.1126/science.1155577 (2008).

6 de Quervain, D. J.-F. *et al.* The Neural Basis of Altruistic Punishment. *Science* **305**, 1254-1258, doi:10.1126/science.1100735 (2004).

7 Gintis, H. A framework for the unification of the behavioral sciences. *Behavioral and Brain Sciences* **30**, 1-16, doi:doi:10.1017/S0140525X07000581 (2007).

8 Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E. & Cohen, J. D. The neural basis of economic decision-making in the ultimatum game. *Science* **300**, 1755-1758 (2003).

9 Pulcu, E. *et al.* Social-economical decision making in current and remitted major depression. *Psychological Medicine*, 1-13 (2014).

10 Gradin, V. *et al.* Abnormal brain responses to social fairness in depression: an fMRI study using the Ultimatum Game. *Psychological Medicine*, 1-11 (2014).

11 Crockett, M. J., Clark, L., Hauser, M. D. & Robbins, T. W. Serotonin selectively influences moral judgment and behavior through effects on harm aversion. *Proceedings of the National Academy of Sciences* **107**, 17433-17438, doi:10.1073/pnas.1009396107 (2010).

12 Ekman, P. & Oster, H. Facial expressions of emotion. *Annual review of psychology* **30**, 527-554 (1979).

13 Young, A. W. *et al.* Facial expression megamix: Tests of dimensional and category accounts of emotion recognition. *Cognition* **63**, 271-313 (1997).

14 Browning, M., Holmes, E. A. & Harmer, C. J. The modification of attentional bias to emotional information: A review of the techniques, mechanisms, and relevance to emotional disorders. *Cognitive, Affective, & Behavioral Neuroscience* **10**, 8-20 (2010).

15 Ma, Q., Hu, Y., Jiang, S. & Meng, L. The undermining effect of facial attractiveness on brain responses to fairness in the Ultimatum Game: an ERP study. *Frontiers in neuroscience* **9**, 77 (2015).

16 Mussel, P., Göritz, A. S. & Hewig, J. The value of a smile: Facial expression affects ultimatum-game responses. *Judgment & Decision Making* **8** (2013).

17 Pulcu, E. & Elliott, R. Neural origins of psychosocial functioning impairments in major depression. *The Lancet Psychiatry* **2**, 835-843 (2015).

18 Browning, M., Behrens, T. E., Jocham, G., O'Reilly, J. X. & Bishop, S. J. Anxious individuals have difficulty learning the causal statistics of aversive environments. *Nature neuroscience* (2015).

19 Nassar, M. R. *et al.* Rational regulation of learning dynamics by pupil-linked arousal systems. *Nature neuroscience* **15**, 1040-1046 (2012).

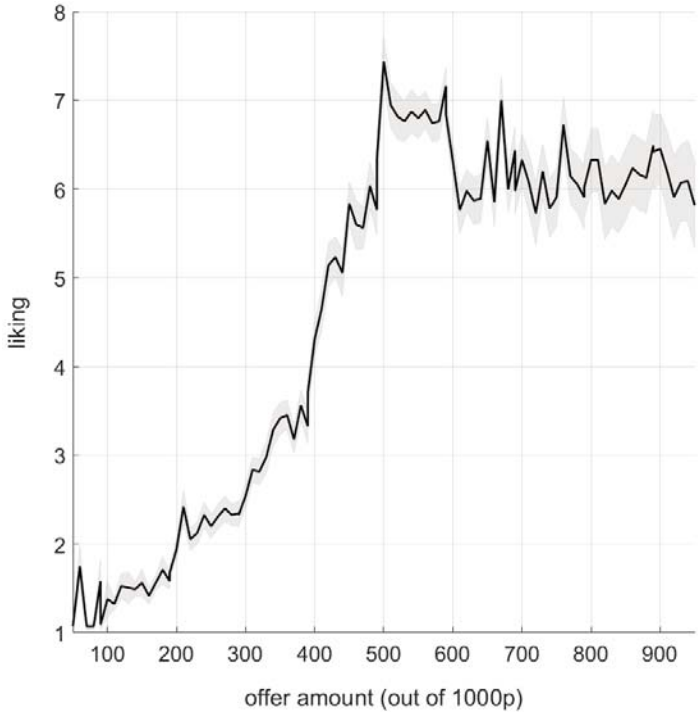
20 Pulcu, E. & Browning, M. Affective bias as a rational response to the statistics of rewards and punishments. *Elife* **6** (2017).

21 Joshi, S., Li, Y., Kalwani, R. M. & Gold, J. I. Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron* **89**, 221-234 (2016).

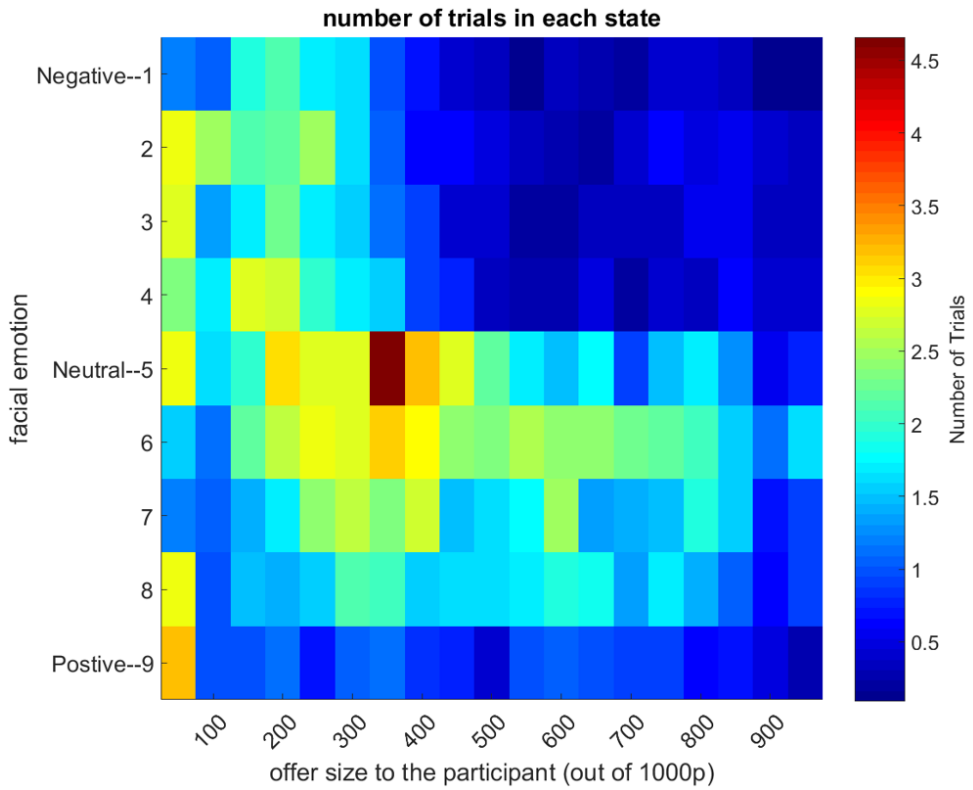
22 Varazzani, C., San-Galli, A., Gilardeau, S. & Bouret, S. Noradrenaline and dopamine neurons in the reward/effort trade-off: a direct electrophysiological comparison in behaving monkeys. *Journal of Neuroscience* **35**, 7866-7877 (2015).
23 Angela, J. Y. & Dayan, P. Uncertainty, neuromodulation, and attention. *Neuron* **46**, 681-692 (2005).
24 Muller, T. H., Mars, R. B., Behrens, T. E. & O'Reilly, J. X. Control of entropy in neural models of environmental state. *Elife* **8**, e39404 (2019).
25 Press, W. H. & Dyson, F. J. Iterated Prisoner's Dilemma contains strategies that dominate any evolutionary opponent. *Proceedings of the National Academy of Sciences* **109**, 10409-10413 (2012).
26 Fehr, E. & Schmidt, K. M. A theory of fairness, competition, and cooperation. *Quarterly journal of Economics*, 817-868 (1999).
27 Stephan, K. E., Penny, W. D., Daunizeau, J., Moran, R. J. & Friston, K. J. Bayesian model selection for group studies. *Neuroimage* **46**, 1004-1017 (2009).
28 Murphy, R. O., Ackermann, K. A. & Handgraaf, M. Measuring social value orientation. *Judgment and decision making* **6**, 771-781 (2011).
29 Pulcu, E. & Browning, M. The misestimation of uncertainty in affective disorders. *Trends in Cognitive Sciences* (2019).
30 Erev, I. & Roth, A. E. Predicting how people play games: Reinforcement learning in experimental games with unique, mixed strategy equilibria. *American economic review*, 848-881 (1998).
31 Hampton, A. N., Bossaerts, P. & O'Doherty, J. P. Neural correlates of mentalizing-related computations during strategic interactions in humans. *Proceedings of the National Academy of Sciences* **105**, 6741-6746 (2008).
32 Yoshida, W., Dolan, R. J. & Friston, K. J. Game theory of mind. *PLoS computational biology* **4**, e1000254 (2008).
33 Yoshida, W., Seymour, B., Friston, K. J. & Dolan, R. J. Neural mechanisms of belief inference during cooperative games. *Journal of Neuroscience* **30**, 10744-10751 (2010).
34 Haroush, K. & Williams, Z. M. Neuronal Prediction of Opponent's Behavior during Cooperative Social Interchange in Primates. *Cell* **160**, 1233-1245 (2015).
35 Schultz, W., Dayan, P. & Montague, P. R. A neural substrate of prediction and reward. *Science* **275**, 1593-1599 (1997).
36 Behrens, T. E., Woolrich, M. W., Walton, M. E. & Rushworth, M. F. Learning the value of information in an uncertain world. *Nature neuroscience* **10**, 1214-1221 (2007).
37 Norbury, R., Mackay, C. E., Cowen, P. J., Goodwin, G. M. & Harmer, C. J. Short-term antidepressant treatment and facial processing: Functional magnetic resonance imaging study. *The British Journal of Psychiatry* **190**, 531-532 (2007).
38 Faber, N. J. Neuromodulation of pupil diameter and temporal perception. *The Journal of Neuroscience* **37**, 2806 (2017).
39 Crockett, M. J. *et al.* Serotonin modulates striatal responses to fairness and retaliation in humans. *Journal of Neuroscience* **33**, 3505-3513 (2013).
40 Murphy, S. E., Norbury, R., O'sullivan, U., Cowen, P. J. & Harmer, C. J. Effect of a single dose of citalopram on amygdala response to emotional faces. *The British Journal of Psychiatry* **194**, 535-540 (2009).
41 Harmer, C. *et al.* Acute SSRI administration affects the processing of social cues in healthy volunteers. *Neuropsychopharmacology* **28**, 148 (2003).
42 Tranter, R. *et al.* The effect of serotonergic and noradrenergic antidepressants on face emotion processing in depressed patients. *Journal of affective disorders* **118**, 87-93 (2009).
43 Schmid, Y. *et al.* Acute effects of lysergic acid diethylamide in healthy subjects. *Biological psychiatry* **78**, 544-553 (2015).

44 Vitiello, B. *et al.* Cognitive and behavioral effects of cholinergic, dopaminergic, and serotonergic blockade in humans. *Neuropsychopharmacology* **16**, 15-24 (1997).
45 Haruno, M. & Frith, C. D. Activity in the amygdala elicited by unfair divisions predicts social value orientation. *Nature neuroscience* **13**, 160-161 (2010).
46 Rilling, J. K., King-Casas, B. & Sanfey, A. G. The neurobiology of social decision-making. *Current opinion in neurobiology* **18**, 159-165 (2008).
47 Behrens, T. E., Hunt, L. T. & Rushworth, M. F. The computation of social behavior. *science* **324**, 1160-1164 (2009).
48 Sonkusare, S., Breakspear, M. & Guo, C. Naturalistic Stimuli in Neuroscience: Critically Acclaimed. *Trends in cognitive sciences* (2019).
49 Harmer, C. *et al.* Effect of acute antidepressant administration on negative affective bias in depressed patients. *American Journal of Psychiatry* **166**, 1178-1184 (2009).
50 Robson, S. E., Repetto, L., Gountouna, V.-E. & Nicodemus, K. K. A review of neuroeconomic gameplay in psychiatric disorders. *Molecular psychiatry*, 1 (2019).
51 Pulcu, E. & Haruno, M. Value computations underlying human proposer behavior in the ultimatum game. *Journal of Experimental Psychology: General* (2019).
52 King-Casas, B. *et al.* Getting to know you: reputation and trust in a two-person economic exchange. *Science* **308**, 78-83 (2005).
53 Prelec, D. The probability weighting function. *Econometrica*, 497-527 (1998).
54 Lopez-Persem, A., Rigoux, L., Bourgeois-Gironde, S., Daunizeau, J. & Pessiglione, M. Choose, rate or squeeze: Comparison of economic value functions elicited by different behavioral tasks. *PLoS computational biology* **13**, e1005848 (2017).
55 Andreoni, J. & Miller, J. Giving according to GARP: An experimental test of the consistency of preferences for altruism. *Econometrica* **70**, 737-753 (2002).
56 Eldar, E. & Niv, Y. Interaction between emotional state and learning underlies mood instability. *Nature communications* **6**, 6149 (2015).
57 Aharon, I. *et al.* Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* **32**, 537-551 (2001).

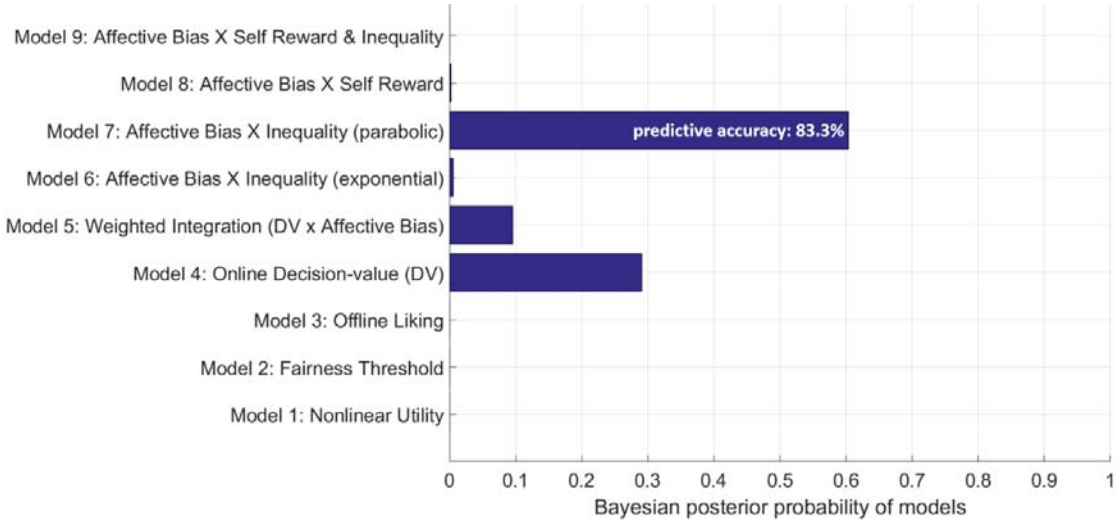
Supplementary Figures



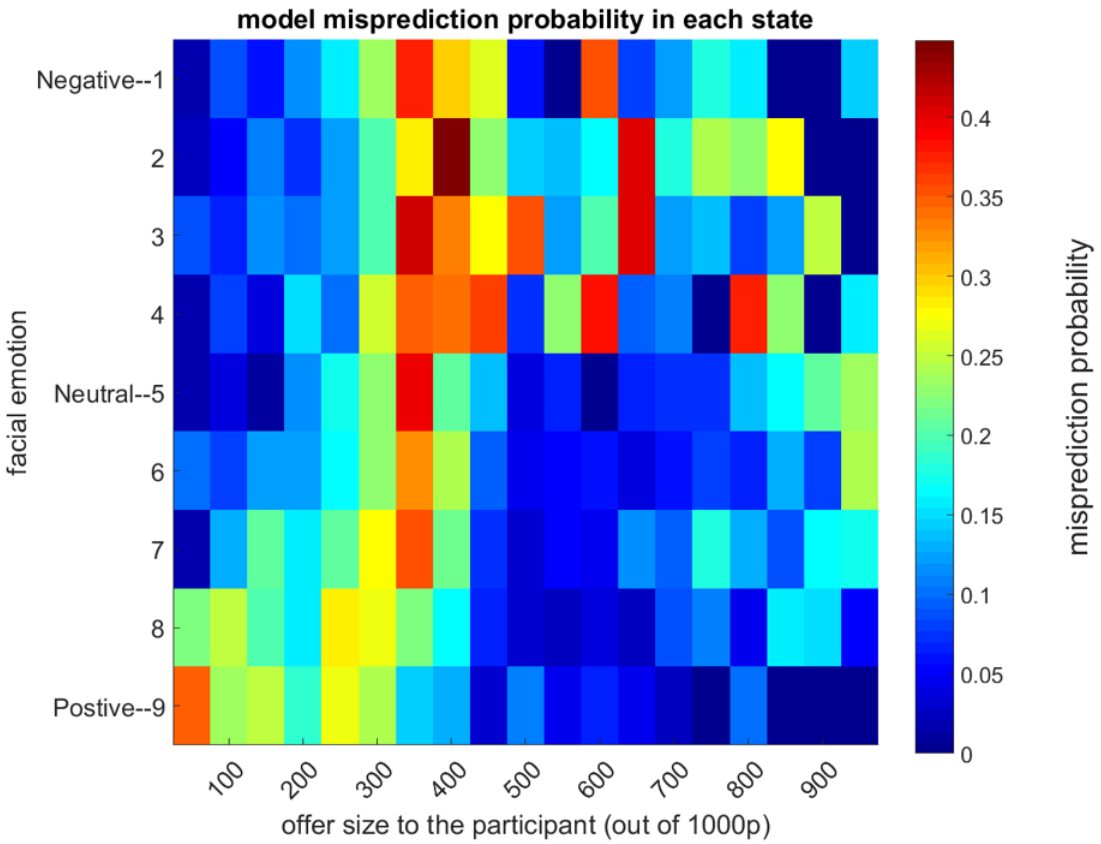
Supplementary Figure 1. Participants' liking ratings monotonically increase from 50p to 500p, which was the point of 50/50 split in the current experimental design. Relatively lower ratings for advantageous offers (>500p) indicate inequality aversion in this cohort. Wider SEM shading around the ratings of advantageous offers indicate a greater individual variability in terms of self-other inequality relative to how unfair offers were rated.



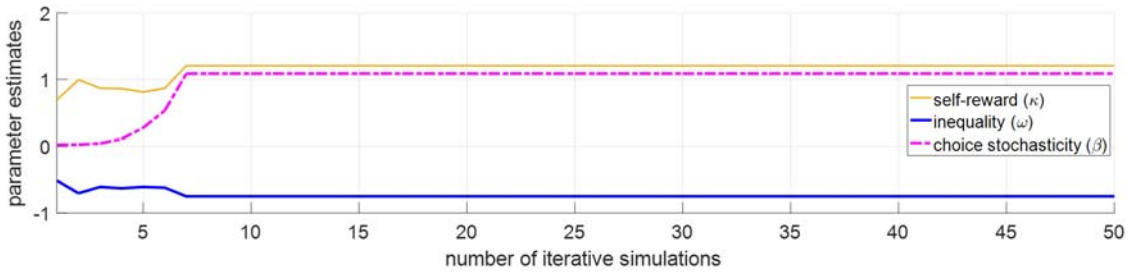
Supplementary Figure 2. Out of 240 trials, average number of trials participants spent in each state-space (i.e. combinations of proposer's facial emotion (y-axis) and offer amounts (x-axis)) represented as a heat map. Colour bar shows the number of trials. On average participants had 12.6±15.9 (mean±SD) trials in the upper right hand quarter (i.e. advantageous offers while the proposer is displaying a negative facial expression).



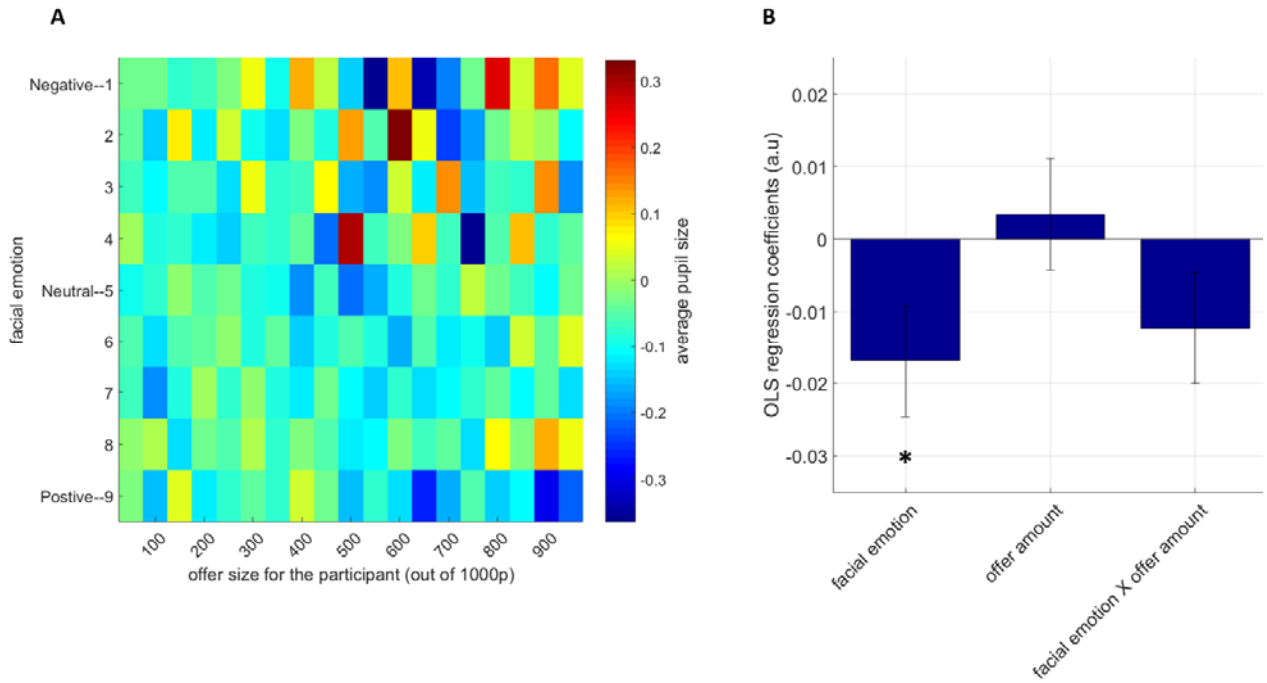
Supplementary Figure 3. Model selection implemented by feeding each model's log-likelihood values in a matrix format (number of participants x number of models) to spm_BMS.m (i.e. the Bayesian Model Selection from SPM12 library), suggests that Model 7 is most likely to be the generative model for the observed data (based on model exceedance probabilities). This model suggests that social affective biases selectively act on the inequality term in a parabolic form.



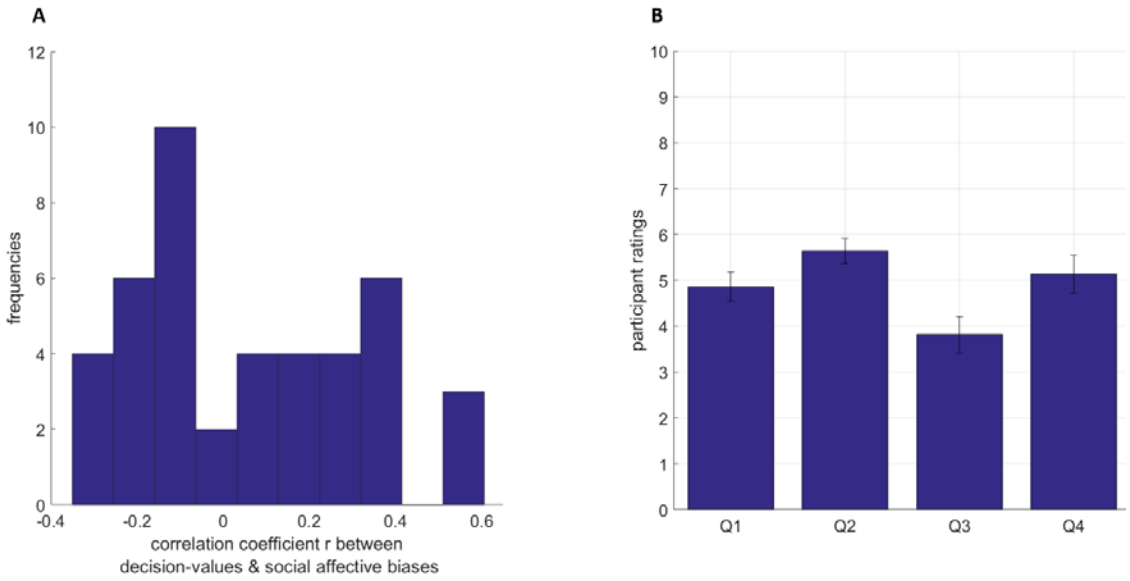
Supplementary Figure 4. Misprediction probabilities of the best-fitting model over the stimuli space. A regression analysis of the trials mispredicted by the best-fitting model did not show a significant main effect of proposer's facial emotions or the offer amount, indicating that the model does not miss the behavioural effect of faces and the offer amount (Figure 3) in a systematic manner.



Supplementary Figure 5. Stability of parameter estimates in generate-recover simulations. Iterative simulations of the best-fitting model based on the population average of the model parameters on a task environment experienced by a representative subject demonstrate that parameter estimates quickly stabilise. In these simulations choices were generated stochastically by a sigmoid function and the parameters in the current simulation (i+1) were re-estimated based on the generated choices from the previous simulation (i).



Supplementary Figure 6. Average pupil size in the Ultimatum Game. (A). Participants' average pupil size across all possible combinations of proposer's facial emotion (y-axis) and offer amounts (x-axis) represented as a heat map. Colour bar shows the average pupil size after presentation of the offer. **(B)** An OLS regression analysis conducted on the pupil size suggested only a significant main effect of proposer's facial emotion (*p<.05).



Supplementary Figure 7. Relationship between social affective biases and decision-values. (A) The distribution of correlation coefficients *r* between social affective biases and decision-values entered in to the pupillary model. Frequencies on the y-axis indicate the number of participants.

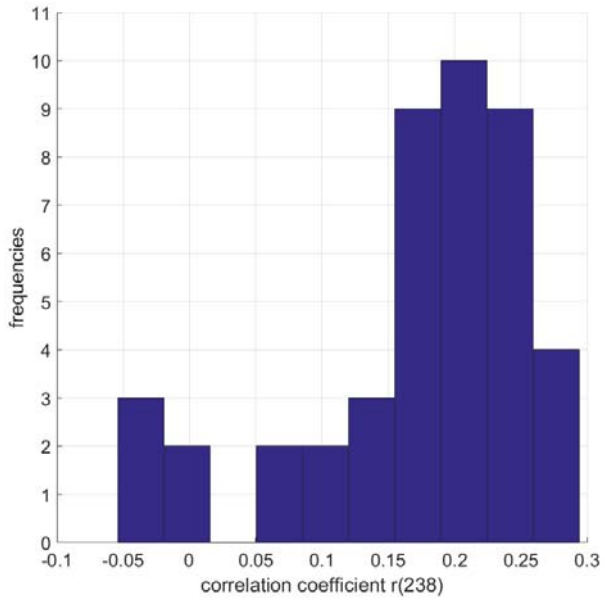
(B) Participants rated the proposer on 4 questions from 0 to 10.

Q1. How much do you think this person cares about rewards to others? (0: does not care at all, 10: cares very much)

Q2. How much would you like this person if you spent 1 hour with him/her in real-life? (0: strong dislike, 10: very likeable)

Q3. How many people do you know in real life who resembles this person (not physical appearance)? (number 0-10)

Q4. How socially close do you feel towards those people that you know? (0: not close at all, 10: very close).



Supplementary Figure 8. Relationship between surprise associated with offers and the actual offer amount. Distribution of correlation coefficients between the surprise regressor generated by the Bayesian filter uniquely for each participant and the vector of offer amounts observed by the participant throughout the task. Frequencies on the y-axis indicate the number of participants.