



Neural substrates underlying the tendency to accept anger-infused ultimatum offers during dynamic social interactions



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ABSTRACT

In managing our way through interpersonal conflict, anger might be crucial in determining whether the dispute escalates to aggressive behaviors or resolves cooperatively. The Ultimatum Game (UG) is a social decision-making paradigm that provides a framework for studying interpersonal conflict over division of monetary resources. Unfair monetary UG-offers elicit anger and while accepting them engages regulatory processes, rejecting them is regarded as an aggressive retribution. Ventro-medial prefrontal-cortex (vmPFC) activity has been shown to relate to idiosyncratic tendencies in accepting unfair offers possibly through its role in emotion regulation. Nevertheless, standard UG paradigms lack fundamental aspects of real-life social interactions in which one reacts to other people in a response contingent fashion. To uncover the neural substrates underlying the tendency to accept anger-infused ultimatum offers during dynamic social interactions, we incorporated on-line verbal negotiations with an obnoxious partner in a repeated-UG during fMRI scanning. We hypothesized that vmPFC activity will differentiate between individuals with high or low monetary gains accumulated throughout the game and reflect a divergence in the associated emotional experience. We found that as individuals gained more money, they reported less anger but also more positive feelings and had slower sympathetic response. In addition, high-gain individuals had increased vmPFC activity, but also decreased brainstem activity, which possibly reflected the locus coeruleus. During the more angering unfair offers, these individuals had increased dorsal-posterior Insula (dpl) activity which functionally coupled to the medial-thalamus (mT). Finally, both vmPFC activity and dpl-mT connectivity contributed to increased gain, possibly by modulating the on-going subjective emotional experience. These ecologically valid findings point towards a neural mechanism that might nurture pro-social interactions by modulating an individual's dynamic emotional experience.

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Introduction

In human relationships, interpersonal conflicts are almost inevitable, occurring whenever two or more interdependent individuals disagree or have opposing goals, and often result in a surge of aggression and violence (De Dreu et al., 2007; Van Kleef, 2010; Forgas et al., 2011). The dynamics of interpersonal conflict evoke strong emotions, most typically anger, which tends to progressively escalate and further fuels the conflict. While anger and aggression are considered as inherent survival responses in animals, humans are endowed with the capability to regulate such negative emotions and thus adapt to different social

situations (Ekman and Davidson, 1994; Davidson et al., 2000; Gross and Thompson, 2007). Consequently, in managing our way through interpersonal conflict, anger regulation may play a crucial role in avoiding violent repercussions and in promoting cooperation. A common framework for studying interpersonal conflict is the Ultimatum Game (UG) – a well established social decision-making paradigm (Güth et al., 1982; Camerer, 2003; Sanfey et al., 2003).

In the UG a proposer decides how to split a sum of money between himself and a responder, who in turn chooses whether to accept or reject the offer. If the responder accepts, both players receive the designated amount of money, but if he rejects, both receive nothing. While focusing on monetary resources, the decision to accept or reject an offer provides an objective measure for the beneficial (i.e., both players gain money) compared to detrimental (i.e., both players lose money) outcome of conflict, respectively. UG studies show that offers of about 25% of the total sum are usually rejected irrespective of the monetary

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sum (Camerer, 2003). Resonating with the now common knowledge that emotions impact decision-making (Lerner et al., 2015), such unequal offers are considered unfair offers that elicit primarily anger, and the rejection is regarded as reflecting an aggressive retribution at one's own personal cost (Pillutla and Murnighan, 1996; Xiao and Houser, 2005). Indeed, it was shown that anger mediated the relationship between the magnitude of offers and acceptance rates such that more anger resulted in decreased acceptance rates (Srivastava et al., 2009). Congruently, psycho-physiological findings showed that unfair UG-offers were associated with increased sympathetic arousal as measured by skin conductance response (SCR; van't Wout et al., 2006) and increased emotional orienting response as measured by heart-rate (HR) deceleration (Osumi and Ohira, 2009; though mixed results were shown by Dunn et al., 2012). An example for individual differences in the emotional response to UG-offers was recently shown in a study in which greater resting HR-variability, a marker of trait emotion regulation capability which was measured before playing the UG, predicted subsequent increased acceptance rates (Dunn et al., 2012). Further support for the role of emotion regulation in one's response to UG-offers stems from findings such that depleting cognitive control resources resulted in decreased acceptance rates (Halali et al., 2014), while explicitly instructing to regulate emotions resulted in increased acceptance rates (van't Wout et al., 2010). Therefore it seems that regulating anger may be important to the acceptance of unfair offers and that people who are better able to regulate anger associated with such offers are more likely to accept and financially benefit from them (Grecucci and Sanfey, 2014). In the current study we focused on the neural substrates that underlay the response to UG-offers using functional Magnetic Resonance Imaging (fMRI). Our goal was to characterize individual differences in the tendency to accept these offers and therefore gain more money, assuming this would reveal neural processes related to the associated emotional experience.

Several processes have been shown to be involved in social decision making, including reward processing, perspective taking, social-norm enforcement and emotion regulation among others (Rilling and Sanfey, 2011). These processes have been largely associated with neural activity in the prefrontal cortex (PFC) and have been specifically implicated in the neural response to being made an offer in the UG, i.e., before the actual decision to accept or reject. The first fMRI study to investigate ultimatum decision-making found that accepting unfair offers was associated with stronger dorsolateral-PFC (dlPFC) activation compared to the anterior-Insula during the offer period, and the reverse pattern was associated with rejection of unfair offers (Sanfey et al., 2003). It was suggested that this might reflect a self-control process exerted by the dlPFC. Indeed, the dlPFC has been associated with domain-general cognitive-control processes (Miller and Cohen, 2001), and specifically with emotion regulation via cognitive reappraisal (Buhle et al., 2013). Congruently, a recent study instructed participants to reappraise their negative emotional response to unfair offers and found that increased activity in a region of the dorsal-PFC positively correlated with acceptance rates (Grecucci et al., 2013). Nevertheless, other studies have suggested that both dlPFC (Knoch et al., 2006; Baumgartner et al., 2011) and anterior-Insula (Corradi-Dell'Acqua et al., 2013) may have a role in fairness enforcement norms, rather than the emotional response per-se. Specifically, dlPFC's involvement in self-control processing of UG-offers might reflect the need to abide to social-norms of what is considered fair.

Interestingly, it has been shown that fair and rewarding offers have been associated with neural activity in a region of the ventro-medial/medial orbital PFC (hereby named vmPFC), and accepting unfair offers of equal absolute value was associated with increased activity in a more lateral region of the ventral-PFC (Tabibnia et al., 2008). Though unfair offers are regularly rejected, accepting such offers might be related to one's valuation of the monetary outcome rather than the perceived fairness of the offer. The vmPFC has been associated with reward valuation, but also with other roles in social and emotional processing

(Bechara et al., 2000; Rolls, 2004; Adolphs, 2009; Mitchell, 2009), and has also been ascribed a specific role in emotion regulation, for example during extinction (Davidson et al., 2000; Quirk and Beer, 2006; Diekhof et al., 2011). In fact, it has been suggested that while the dlPFC is mainly related to voluntary-explicit emotion regulation, the vmPFC is related to automatic-implicit emotion regulation (Phillips et al., 2008; Gyurak et al., 2011). These multiple functionalities have posed difficulty in interpreting the role of the vmPFC during ultimatum decision-making. For example, patients with vmPFC-lesions and an acquired deficit in emotion regulation that played the UG had increased rejection rates compared to controls, suggestive of vmPFC's role in regulating the emotional response to unfair-offers (Koenigs and Tranel, 2007). In contrast, it was suggested that reward sensitivity rather than emotion-regulation per-se was the domain of deficit, since if payment of rewards was in cash immediately after the game, vmPFC-lesion patients did not differ from controls (Moretti et al., 2009). Albeit an additional vmPFC-lesion study suggested that vmPFC's role in accepting unfair offers was related to perspective-taking capabilities (Shamay-Tsoory et al., 2012). Importantly, an fMRI study revealed that individual differences in the tendency to accept unfair offers was related to increased vmPFC activity during unfair offers, which also mediated the relationship between pre-UG testosterone levels, a marker of aggressiveness, and acceptance rates (Mehta and Beer, 2010). While pointing at the role of the PFC in UG behavior, imaging studies have yet to provide a clear indication of the neural substrates involved in the idiosyncratic emotional experience associated with the decision to accept or reject offers in the UG.

Taken together, the UG provides a promising platform for studying individual differences in anger experience and its' regulation within a social decision-making context, representing interpersonal conflict over monetary resources. However, the interaction between players in the UG lacks fundamental characteristics of the naturalistic social dynamics of such an interaction. A true engagement in social interaction occurs when people can communicate with other people in their environment, conveying their feelings, thoughts and intended actions, and adapting themselves in a response-contingent manner (Przyrembel et al., 2012; Schilbach et al., 2013). Yet the vast majority of findings on the neurobiological underpinnings of complex human cognitive-affective phenomena are based on "offline" paradigms during which participants' brains are studied in isolation from other people in the environment. This seems at odds with the notion that emotional episodes occur and emerge mostly via our social interactions (Fischer & van Kleef, 2010). Indeed, during interpersonal conflict these interactions take the form of negotiations which may spiral to personal insults and provocations and are thus an additional source for anger induction. Nevertheless, in most UG studies communication is based on restricted information of offers and decisions. Moreover, most UG studies implement a "single-shot" paradigm in which each offer is from a different, most often a virtual proposer, reducing to almost none the dynamic nature of the interaction. In addition, the induction of anger has been based solely on the magnitude of offers and not on the type of emotional experience which evolves during the interaction. To account for these gaps we modified the UG to a repeated form of the game (Slembeck, 1999), in which participants needed to decide whether to accept or reject offers from the same putative proposer, and incorporated on-line verbal negotiations between the players after each round. During these verbal negotiations participants were confronted with an obnoxious hard-playing confederate proposer, which was in fact a professional actor who improvised with scripted provocations in order to infuse more genuine and interpersonal anger to the conflict.

In the current study, participants in the scanner played 10 UG-rounds with the same proposer who was outside the scanner, and were generally informed they could utilize negotiations to improve their subsequent offers. Unbeknownst to them, the provocations during negotiations were in concert with a sequence of predefined offers allotted from a pot of 20 Israeli New Shekel (ILS) per offer (1 ILS \approx 0.3 USD). Therefore, participants were led to believe that their verbal negotiations

had an influence on subsequent offers from the proposer, but in fact the purpose of these negotiations was to emphasize the anger probing nature of the game in a realistic and interpersonal fashion. In addition to blood oxygen level-dependent (BOLD) brain activity measured with fMRI, we simultaneously obtained SCR to estimate sympathetic arousal. Following scanning, and to characterize the emotional experience unfolded during our modified-UG, participants were asked to report their feelings on a round-by-round basis, based on the Geneva Emotion Wheel (GEW; Scherer, 2005). Our modified-UG was divided into two seamless fMRI scans to reduce head-movement artifacts. The dynamic experience generated in our modified-UG was assessed by comparing both emotional ratings and brain activity between the two halves of the game, and also by functional connectivity analysis. Overall, we hypothesized that participants will report more anger compared to other

negative emotions and compared to positive emotions, and expected increased anger in the second half of the game compared to the first. While we did not preclude the relevance of factors such as reward sensitivity in accepting UG-offers, we assumed that gaining money throughout our anger-infused modified-UG would reflect at least in part a trait-like capability to regulate these angry emotions within the entire interpersonal conflict scenario. We thus characterized participants based on the median split of the total monetary gain accumulated throughout the game (hereby termed high- or low-gainers). We hypothesized that high-gainers would report less anger, and exhibit less sympathetic arousal compared to low-gainers. In view of vmPFC's association with individual differences in UG-behavior and its suggested role in implicit emotion regulation, we also hypothesized that increased activity in this region would relate both to high-gain and reduced anger.

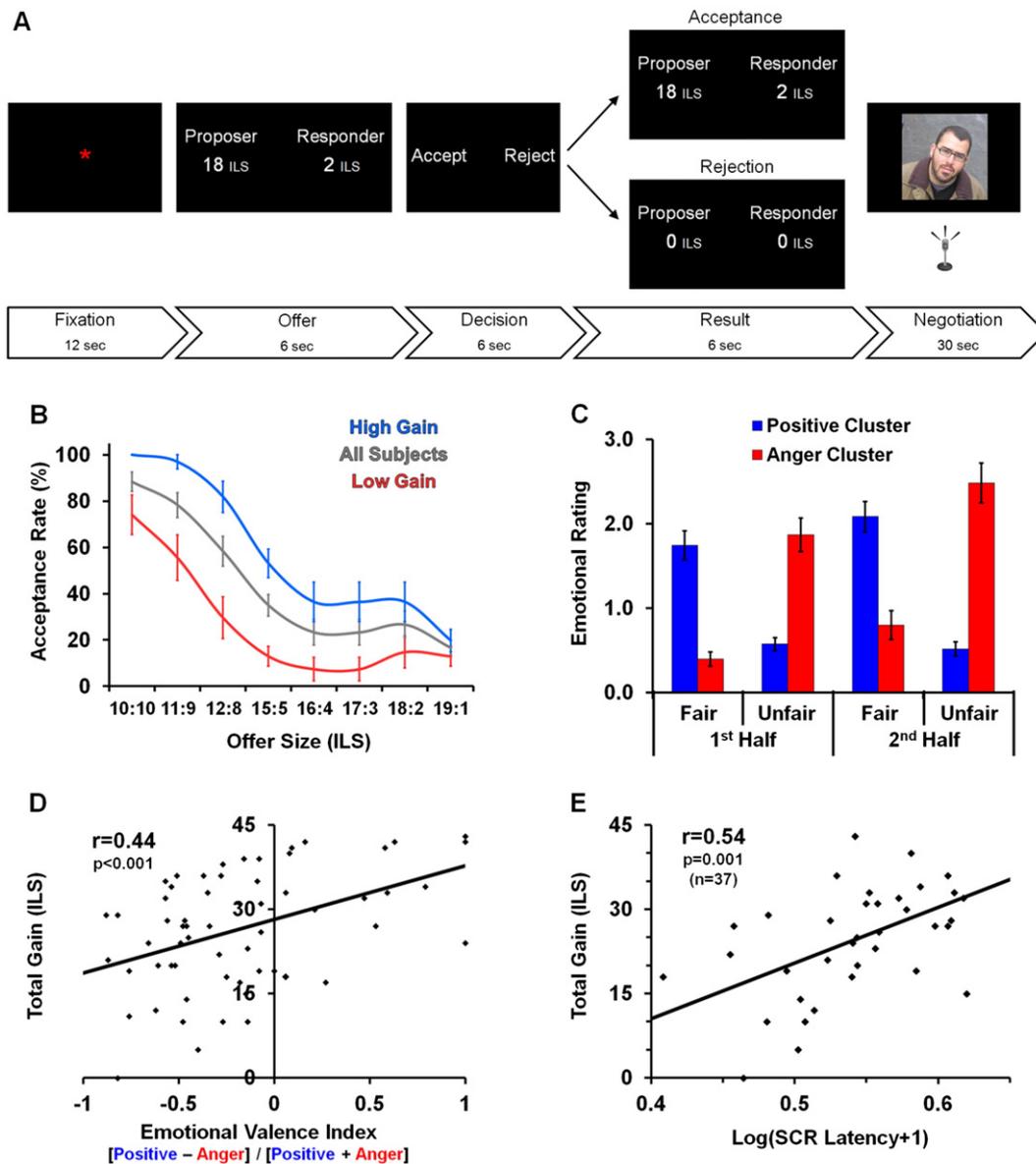


Fig. 1. Experimental design, behavioral and physiological results. (A) The experimental design of one round in our modified-UG. Each round began with a fixation period, supposedly the time in which the proposer decided how to split the sum of 20 Israeli New Shekel (ILS). Participants then saw the offer, decided whether to accept or reject and then viewed the result of their decision. Verbal negotiations followed and began when a fictitious picture appeared, supposedly belonging to the other player. This sequence was repeated 10 times in total. (B) Acceptance rates (error bars denote mean \pm s.e.m.) decreased with offer size for all subjects (gray; $n = 60$, 26.55 ± 10.29 ILS, total-gain mean \pm s.d.) but for each offer size (except 19:1) were higher for the High-Gain group (blue; $n = 33$, 34.24 ± 5.15) compared to the Low-Gain group (red; $n = 27$, 17.15 ± 6.39). (C) Fair offers induced more positive emotions and less anger, unfair offers not only showed the reverse pattern, but also induced less positive emotions and more anger compared to fair offers (Tukey's $p < 0.001$ two-tailed for all these comparisons). Additionally, anger increased in the second half of the game for both fair ($p = 0.006$) and unfair ($p < 0.001$) offers. (D) Total-gain accumulated in the game was positively related to participants' Emotional Valence Index (EVI), calculated as the ratio between [Positive Cluster - Anger Cluster] and [Positive Cluster + Anger Cluster], and (E) to the latency of the first above threshold Skin Conductance Response (SCR).

This also corresponds to the fact that we did not explicitly inform participants about the expected emotional experience during the game, and neither instructed them to regulate it. Importantly, while regulatory processes may occur at any time-point during the modified-UG, we focused our analyses on the offer period because that is the “moment of truth” in which one needed to confront the actual monetary-offer and prepare for making the decision which will influence both himself and the proposer, and would be a basis for subsequent negotiations. Finally, since unfair offers induce more anger, we expected the behavioral and neural effects to be more accentuated during such offers compared to fair offers.

Materials and methods

Participants

Sixty males (age 18.62 ± 0.88 , mean \pm s.d.) were recruited on a voluntary basis. Twenty-two (age 18.18 ± 0.39) civilians were from

Israeli civil-service programs and 38 (age 18.87 ± 0.99) soldiers were just enlisted to military service and designated to a combat-unit in the Israeli Defense Force (IDF). All participants provided written informed consent and the study was approved by the Institutional Ethics Committee of the Tel-Aviv Sourasky Medical Center and of the IDF. These two groups were sampled as part of a prospective research program aimed to study the effect of military training on emotion regulation and its relation to the risk to develop traumatic stress following military exposure. Participants were not explicitly exposed to the emotion regulation aspect of the study. The current study is from the first time-point, in which participants were sampled at the first month of their respective programs (i.e., beginning of military training for the soldiers). Participants had no reported history of psychiatric or neurological disorders and had normal or corrected-to-normal vision. Thirteen additional participants were discarded from the final analysis: four soldiers and one civilian since they expressed suspicion of the manipulation, seven soldiers did not partake in the anger induction manipulation and one soldier decided to abort participation in the fMRI scan. Since there were

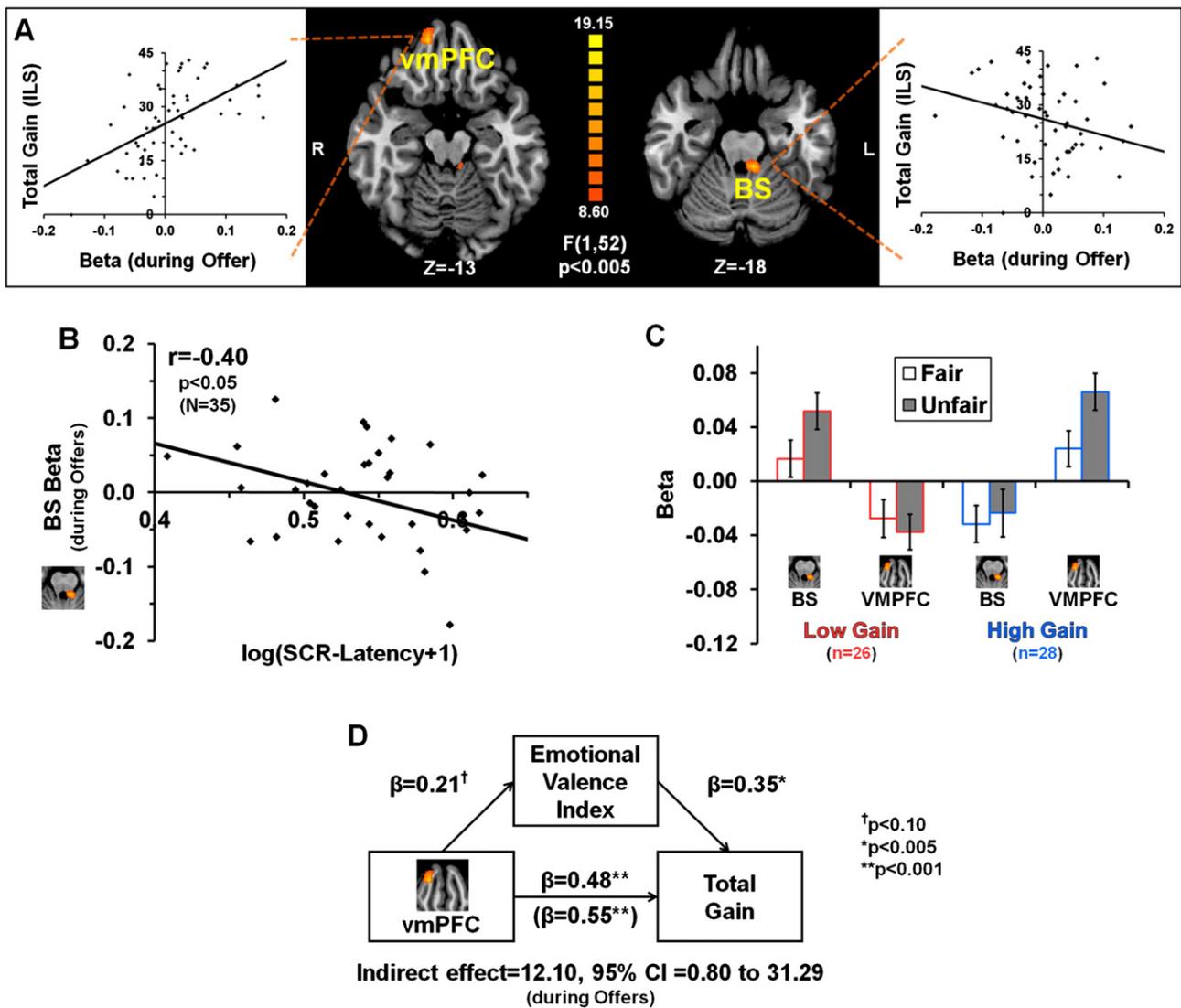


Fig. 2. During the offer periods, activity in the vmPFC and BS differentiated between gain-groups. (A) Gain-groups main effect (GLM with random effects, $n = 54$) found activity in a ventral region of the PFC (vmPFC; $x, y, z = 14, 49, -12$) and in the brainstem (BS; $x, y, z = -7, -35, -18$) illustrated at a threshold of $p < 0.005$ (uncorrected) and a minimal cluster size of 10 contiguous functional voxels. vmPFC activity (left) increased and BS activity (right) decreased with participants' increased total-gain. Brain coordinates are in Talairach space. (B) BS activity negatively related to SCR-latency. (C) vmPFC and BS exhibited a dissociated pattern of activation. High Gain group displayed increased vmPFC activation and decreased BS activation during unfair offers, while Low-Gain group displayed the reverse pattern of activation (Tukey's $p < 0.001$ two-tailed for all these comparisons). (D) Mediation model depicting a significant indirect path from vmPFC to total-gain through Emotional Valence Index (EVI), during the offer periods. Such an indirect effect was not found for the BS. β indicates standardized regression coefficients and β in parentheses indicates the coefficient between vmPFC activity and total-gain before controlling for EVI. Indirect effect indicates the bias-corrected bootstrap coefficient and its' constructed 95% confidence interval (CI).

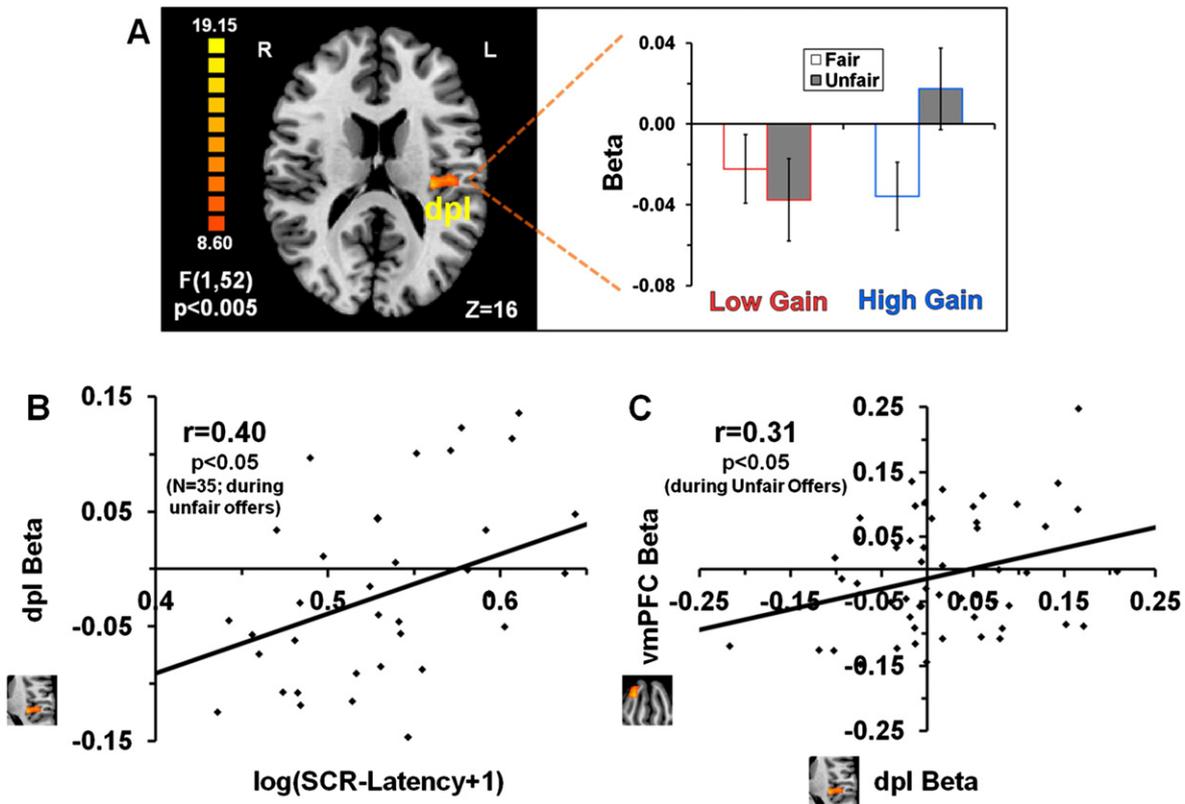


Fig. 3. During unfair offers compared to fair offers, dpl activity differentiated between gain-groups. (A) Gain-groups \times fairness interaction effect (GLM with random effects, $n = 54$) revealed activity in the dorsal posterior Insula (dpl; $x, y, z = -31, -23, 18$) illustrated at a threshold of $p < 0.005$ (uncorrected) and a minimal cluster size of 10 contiguous functional voxels. dpl activity increased during unfair offers compared to fair offers, but only for the High-Gain group. During unfair offers, dpl activity positively related to (B) SCR-Latency and to (C) vmPFC activity.

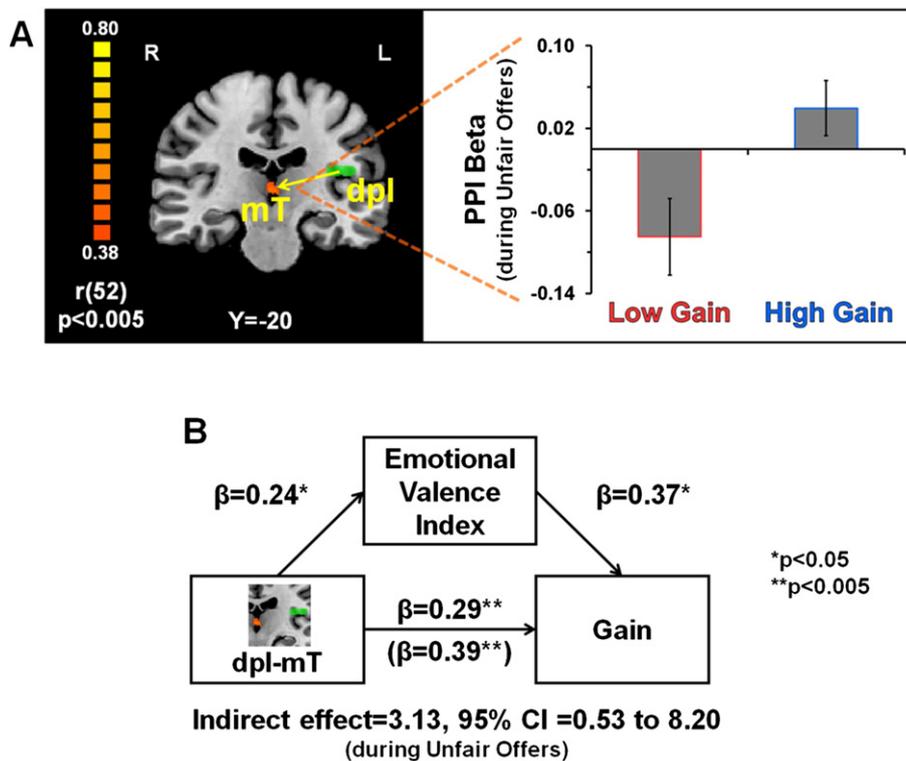


Fig. 4. During unfair offers, dpl-mT functional connectivity differentiated between gain-groups. (A) Using dpl as a seed region for psycho-physiological interaction (PPI) during unfair offers (GLM with random effects, $n = 54$) revealed an increase in functional connectivity between the dpl and the medial Thalamus (mT; $x, y, z = -1, -23, 5$), illustrated at a threshold of $p < 0.005$ (uncorrected) and a minimal cluster size of 10 contiguous functional voxels, for the High-Gain group, but not for the Low-Gain group. (B) Mediation model depicting a significant indirect path from dpl-mT connectivity to gain accumulated during the unfair offers of the game, through the EVI measure, also during the unfair offers.

no differences between civilians and soldiers in all measures they were considered as a single group for this time point of the study (see the [Results](#) section).

Modified Ultimatum Game

We modified a previously used fMRI UG-protocol (Sanfey et al., 2003) by incorporating 30 second verbal negotiations between the participant and a putative proposer following each UG-round (Fig. 1A; Inline Supplementary Movie S1). The proposer was in fact one of three professional actors (counterbalanced between participants) trained with scripted improvisations (see below) to further evoke anger and intensify conflict. The negotiations gave participants the possibility to express themselves spontaneously in reaction to the terminated UG-round and solicit the putative proposer regarding the next round. Similar modifications have previously been used but not with on-line verbal communication, rather computer-based messaging (e.g., Xiao and Houser, 2005). Participants were led to believe that negotiations enabled them to bargain with the proposer to maximize monetary gain but no indications were made regarding the emotional experience which might be associated with these negotiations. Participants were also explained that to avoid any pre-game agreements between the two players they would never meet. Each participant was photographed and told the photo would be used as a cue for starting negotiation. During scanning the participants saw a photo of the proposer and their own photos were only used in pre-scan simulation practices. Participants played the responder and were led to believe that their decisions to accept or reject (via a button press) were made vis-à-vis offers by a proposer who supposedly split 20ILS in real-time. In reality, four pre-determined sequences of both fair (10:10, 11:9, 12:8) and unfair (2 × 15:5, 16:4, 17:3, 18:2, 2 × 19:1) offers were counterbalanced between participants (Inline Supplementary Table S1). Since there were no differences between these sequences in all measures they were collapsed across all analyses (see the [Results](#) section). In addition, we expected verbal negotiations to entail increased head-movements and thus divided the game into two seamless 5-round fMRI scans to reduce movement effects on the BOLD signal (see the [fMRI data acquisition and analysis](#) section).

Inline Supplementary Movie S1 and Table S1 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

Before starting the game, a quick introduction was conducted between the two players via the shared audio system. Participants were described as civilians or soldiers and the putative proposers as volunteering students. Subsequently, the experimenter exposed a bogus high-score table to increase competitiveness and motivation. In accordance with the Institutional Ethics Committee demands, there were no actual material payoffs of any kind. We assumed that portraying the UG as a game in which one should aim for a high total-gain of money (even if fictive) and reach the high-score table is an adequate context to motivate participation, especially in view of the prospective nature of our study. This also goes hand-in-hand with our division into high-gain and low-gain participants. Previous findings showed no difference in acceptance rates of fair and unfair offers among healthy subjects when comparing abstract to cash rewards while interacting with a supposedly human proposer (Moretti et al., 2009). To ensure interest and motivation in playing the game we asked participants to rate their desire to gain money upon completion of the task (on a 0 to 10 scale) and found high ratings across all subjects (6.47 ± 2.71), with no influence of recruitment group (soldier/civilian), gain-group (low/high) nor the interaction between them ($p > 0.40$).

Actor training

Three actors playing as proposers received a thorough explanation regarding the UG and were instructed to be generally antagonistic and uncooperative while incorporating scripted provocations in a realistic

fashion during verbal negotiations, in congruence with the pre-programmed sequence of offers. Please see Supplementary methods for additional information on actor training. Since there were no differences between the three actors in all measures they were collapsed across all analyses (see the [Results](#) section).

Emotional rating

An iterated version of the Geneva Emotion Wheel (GEW; Scherer, 2005) scheme was used to obtain post-scan subjective reports of the emotional experience during the modified-UG, on a round-by-round basis and in accordance with participants' actual decisions. The retrospective nature of the report aimed to avoid interference with the spontaneous interaction between participants and actors. Similar post-scan dynamic ratings of emotional experiences have previously been performed in our lab with strong reliability and validity (Raz et al., 2012), as in other UG experiments (Osumi and Ohira, 2009; Dunn et al., 2012). The GEW comprises 16 emotions arranged in a circular pattern based on two axes, valence (positive/negative) and potency (high/low): Pride, Elation, Happiness, Satisfaction, Relief, Hope, Interest, Surprise, Anger, Hostility, Contempt, Disgust, Shame/Guilt, Boredom, Sadness and Anxiety. In our version of the GEW, participants received a print-out of 30 screen-shots that traced each offer, result and negotiation periods in the exact sequence of UG-rounds as played in the scanner. Adjacent to each print-screen was a GEW and participants were instructed to rate each emotion on a 7-point intensity scale from 0 (none) to 6 (very high), in relation to how they felt in that exact period during the actual game in the scanner. Specifically for the negotiation screen-shots, which featured the photo of the putative-proposer, participants were generally instructed to try and replicate the content of interaction and rate the emotional experience accordingly.

Trait questionnaires

The prospective study included various trait measures of which we provide general details in Inline Supplementary Table S2 (Inline Supplementary Table S2).

Inline Supplementary Table S2 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

Skin conductance data acquisition and analysis

Skin conductance (SC) was simultaneously recorded during fMRI scans using the GSR-MR BrainAmp-MR ExG system (Brain Products). Raw data was sampled at 5 kHz and recorded using the BrainVision Recorder software (Brain Products). SC was recorded via two Ag/AgCl electrodes filled with isotonic NaCl unibase electrolyte attached to the volar surface of the second phalanx of the second and third fingers of the non-dominant hand. Pre-processing the data consisted of MR gradient artifacts removal using a FASTR algorithm and then down-sampling the signal to 250 Hz. Technical malfunctions led to the availability of only 37 participants (low-gainers = 18, high-gainers = 19). Analysis utilized EEGLAB 6.01 software package (Schwartz Center for Computational Neuroscience, University of California, San Diego) for cardio-ballistic artifact removal. Ledalab software (<http://www.ledalab.de/>) was used to differentiate between the tonic and phasic components of SC signal, changing it into discrete events which enabled to analyze SC in response to specific periods (Benedek and Kaernbach, 2010a,b). While there are different approaches for the analysis of SC, it has recently been shown that ledalab is comparable to other such approaches (Green et al., 2014). The data was framed within a response time-window of between 1 and 5 s after the stimuli appeared. We inspected SC responses (SCR) during the offer periods. Minimal threshold was set at 0.02 microsiemens (μS) and a log transformation was incorporated to normalize the data. Two SC parameters were analyzed: (1) SCR-intensity — the average skin conductance response within the response

time-window and (2) SCR-latency – the onset in seconds of the first SCR in the response time-window. SCR-latency is less common but was shown to reflect sympathetic arousal similarly to SCR-intensity (Witvliet and Vrana, 1995). The first offer had stronger SCR-intensity compared to all other offers [$p < 0.05$ compared to almost all other offers]. There was no difference between gain-groups in this first offer [intensity: Student's $t_{df=35} = -0.06$, $p = 0.95$, *Cohen's d* = -0.02 ; latency: $t_{33} = -0.01$, $p = 0.99$, *Cohen's d* = 0.00], thus we discarded data from the first offer from all subsequent analyses.

fMRI data acquisition and analysis

Brain imaging was performed by a GE 3 T Signa Excite scanner using an 8-channel head coil at the Wohl Institute for Advanced Imaging, Tel-Aviv Sourasky Medical Center. Functional whole-brain scans were performed with gradient echo-planar imaging (EPI) sequence of functional T2*-weighted images (TR/TE = 3000 / 35 ms; flip angle = 90°; FOV = 200 × 200 mm; slice thickness = 3 mm; no gap; 39 interleaved top-to-bottom axial slices per volume). Anatomical T1-weighted 3D axial spoiled gradient (SPGR) echo sequences (TR/TE = 7.92/2.98 ms; flip angle = 15°; FOV = 256 × 256 mm; slice thickness = 1 mm) were acquired to provide high-resolution structural images.

Preprocessing and statistical analyses were conducted using BrainVoyager QX version 2.4 (Brain Innovation). Each scan began with 10 volumes (30 s) of blank screen which were removed to allow for signal equilibrium. Subsequently, slice scan time correction was performed using cubic-spline interpolation. Head motions were corrected by rigid body transformations, using 3 translation and 3 rotation parameters and the first image served as a reference volume. Trilinear interpolation was applied to detect head motions and sinc interpolation was used to correct them. The temporal smoothing process included linear trend removal and usage of high pass filter of 1/128 Hz. Functional maps were manually coregistered to corresponding structural maps and together they were incorporated into 3D data sets through trilinear interpolation. The complete data set was transformed into Talairach space and spatially smoothed with an isotropic 6 mm FWHM Gaussian kernel. Applying a criterion for exclusion based on excessive head-movements at 1 voxel (3 mm/3°) left us with only 40 participants which had both fMRI scans of the game. Increasing the criterion by an additional 1 mm/1° increased the number of participants to 54 (low-gainers = 26, high-gainers = 28). There were no differences in results between these two criterions (Inline Supplementary Figure S1), thus our results are presented for the larger sample. We found no difference between the two gain-groups' average peak head-movements (across both fMRI runs) in both translation ($t_{52} = 1.62$, $p = 0.11$, *Cohen's d* = 0.44) and rotation ($t_{52} = 1.65$, $p = 0.10$, *Cohen's d* = 0.45) parameters. Four additional subjects had excessive head-movements on one or both fMRI scans and were discarded from analysis, and two more participants were discarded due to scanner technical malfunctions during acquisition.

Inline Supplementary Fig. S1 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

A single whole-brain random effects General Linear Model (GLM) was computed which included eight regressors, two for each period of the game (offer, decision, result, negotiation) to represent the two fMRI scans. Regressors were convolved with a canonical hemodynamic response function. Additional nuisance regressors included the head-movement realignment parameters and the time course of averaged activity in cortical white-matter. The fixation period of both scans was used as baseline. We also incorporated a gray-matter mask and corrected for temporal autocorrelations using a second-order autoregressive model. We then submitted the BOLD brain activity during the offer period to a 2 (gain-groups: Low/High) × 2 (fairness of offer: fair/unfair) × 2 (game-half: 1st/2nd) mixed-model analysis of variance (ANOVA). We focused on effects of the gain-group which would specify brain regions related to the tendency to accept or reject

offers during the game. Correction of brain activation maps for multiple comparisons was performed by setting a voxel-level threshold at $p < 0.005$ (uncorrected) with a minimal cluster-size of 10 contiguous functional voxels (where each voxel corresponds to a functional volume of 3 × 3 × 3 mm) thus producing a desired balance between Types I and II error rates (Lieberman and Cunningham, 2009). To further decrease the likelihood of Type I errors, we extracted mean parameter estimates (beta values) for further analyses only for those regions of interest (ROIs) whose peak voxel had a false discovery rate (FDR) of $\alpha = 5\%$. Beta values were averaged across the entire ROI voxels and for each experimental condition separately.

Functional connectivity analysis

A whole-brain psycho-physiological interaction (PPI; O'Reilly et al., 2012) random effects GLM analysis was conducted to test functional connectivity of the functionally identified ROIs. Regressors included: (1) the psychological variable – the original regressor of the specific experimental condition (2) the physiological variable – the time course activity in the seed ROI and (3) the interaction variable – an element-by-element product of the psychological and physiological variables. The psychological and physiological variables were included as confounds of no-interest (in addition to the nuisance regressors mentioned above). Correction for multiple comparisons and ROI analysis followed the same steps as detailed above.

Mediation analysis

Mediation analysis enables to statistically test whether the indirect path between an independent and a dependant variable passes fully or partially through a third mediating variable (Shrout and Bolger, 2002; Preacher and Hayes, 2004, 2008). An indirect path may reveal an otherwise inexistent direct relation between two variables. Using bootstrap procedures to test significance of indirect paths is especially important for small to medium sized samples because the estimate of the indirect effect cannot be assumed to distribute normally and because otherwise such samples lack power. Statistical significance is based on a confidence interval. The range of the bootstrapped distribution (here based on 10,000 iterations) of the confidence interval provides for the statistical significance as long as it does not contain zero, since the null hypothesis is that the indirect effect is non-existent, i.e., equal to zero.

Audio equipment

OptoAcoustics™ adaptive and automatic noise canceling FOMRI-III™ optical microphone and matching insulated headphones with built-in loudspeakers were used to minimize interferences during verbal negotiation within the MR scanner.

Procedure

Upon arrival, participants received an explanation of the planned prospective study and experimental procedures, including specific UG-related instructions. After signing an informed consent and completing the trait personality questionnaires, participants were assembled with SC electrodes and then entered the MRI scanner in which the current UG-paradigm was the last active paradigm. With each of the two scans consisting of 30 s of blank followed by five one-minute UG-rounds, the entire paradigm lasted for 11 min. Upon exiting the MRI participants completed the emotional rating. Debriefing was conducted at the end of the prospective research program.

Results

Acceptance rates and total-gain

We averaged acceptance rates (in percentage) for the two fairness categories (fair/unfair) and submitted them to a 2 (recruitment-group: soldiers/civilians) \times 4 (sequence of offers: 1/2/3/4) \times 3 (actor: 1/2/3) mixed-model ANOVA. In line with standard UG results, a main effect of fairness was revealed [$F_{1,36} = 144.83$, $p < 0.001$, $\eta_p^2 = 0.79$] such that fair offers (75.00 ± 26.49) were accepted more than unfair offers (25.24 ± 21.91). None of the between-subject factors influenced this result (or any of the below detailed results; Inline Supplementary Table S3) and therefore were collapsed across all subsequent analyses. In accordance with our assumption and independently from the fairness of offers, we classified participants as high-gainers (HGs; $n = 33$) or low-gainers (LGs; $n = 27$) based on the median of total-gain (27.00 ILS out of maximum 48.00 ILS; mean = 26.55 ± 10.29), reflecting an objective measure of the final outcome of the modified-UG. Though total-gain and overall acceptance rates highly correlated (Pearson's $r = 0.91$, $p < 0.001$), total-gain is a more accurate measure for individual differences (e.g., one who only accepts a 10:10 and 4:16 offers would have a different gain but equal acceptance rate to one who accepted a 9:11 and 8:12 offers). Confirming the LG/HG division, the average total-gain of LGs (17.15 ± 6.40) was lower than HGs (34.24 ± 5.15) [$t_{58} = 131.67$, $p < 0.001$, *Cohen's d* = 2.95]. To test the difference in the pattern of acceptance rates per magnitude of offer between the two groups we performed a repeated-measures ANOVA per offer-size (10:10, 11:9, 12:8, 15:5, 16:4, 17:3, 18:2, 19:1) with gain-groups (LGs/HGs) as between-subject factor. This revealed a main effect of offer-size [$F_{7,406} = 32.63$, $p < 0.001$, $\eta_p^2 = 0.36$], a main effect of gain-group [$F_{1,58} = 87.77$, $p < 0.001$, $\eta_p^2 = 0.60$] and an interaction effect [$F_{7,406} = 2.12$, $p = 0.04$, $\eta_p^2 = 0.04$]; Fig. 1B) which indicated that although acceptance rates decreased with offer size, HGs exhibited higher acceptance rates than LGs for each offer-size [uncorrected $p < 0.05$, two-tailed, except for 19:1 for which there was no difference].

Inline Supplementary Table S3 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

Emotional rating

We examined the average reported emotions for all periods and all rounds of the retrospective emotional rating based on the two GEW-axes of potency (high/low) and valence (positive/negative) and found a significant interaction [$F_{(1,36)} = 29.65$, $p < 0.001$, $\eta_p^2 = 0.45$] which indicated, as expected, that the negative high potency cluster which includes Anger, Hostility, Contempt and Disgust (hereby named anger-cluster) was the dominant category of emotions, compared to all other categories [1.57 ± 1.34 ; Tukey's $p < 0.001$, two-tailed]¹. At the same time, both positive clusters did not differ from each other [low = 0.95 ± 0.76 ; high = 0.85 ± 0.82 ; $p = 0.85$] and the negative low potency cluster was the least reported of all emotion clusters [0.49 ± 0.60 , $p < 0.05$]. Subsequent analyses were focused on the relation between the anger-cluster compared to an all-positive-emotions cluster. To further validate these clusters of emotions we conducted k-means clustering for two, three and four clusters. In all these cases the anger-cluster was separated from all other emotions and all positive emotions were clustered together. To assess the impact of our anger-infusion manipulation we tested whether there was a difference in emotional rating in these

two emotion-clusters (positive/anger) between the different periods of the game (offer, result, negotiation). We found a significant interaction [$F_{(1,118)} = 19.94$, $p < 0.001$, $\eta_p^2 = 0.25$] which revealed that the result period was generally less angering (1.26 ± 1.39) than both the offer (1.70 ± 1.30 ; $p < 0.001$) and the negotiation periods (1.74 ± 1.49 ; $p < 0.001$). However, there was no difference in emotional rating between the offer and negotiation periods for both the anger [$p = 0.99$] and the positive [offer = 0.94 ± 0.71 ; negotiation = 0.79 ± 0.79 ; $p = 0.36$] emotion-clusters. In addition, there was a strong correlation between emotional ratings of the offer and negotiation periods for both anger [$r = 0.91$; $p < 0.001$] and positive [$r = 0.91$; $p < 0.001$] clusters of emotion. Results thus far generally indicate that our modified-UG indeed induced anger, which at least as subjectively reported, was comparable between the offer and negotiation periods. Since our analysis of the physiological and neural measures was focused on the offer period, subsequent analyses used the emotional rating specifically during the offer period.

We next averaged the ratings in the two emotion clusters (positive/anger) for the two halves of the game (1st/2nd) and submitted them to a 2 (fairness: fair/unfair) \times 2 (gain-groups: LGs/HGs) mixed model ANOVA. As expected, a significant interaction between emotion clusters, fairness of offers and the two halves of the game [$F_{(1,58)} = 9.53$, $p = 0.003$, $\eta_p^2 = 0.14$; Fig. 1C], indicated that unfair offers were associated with more anger and less positive emotions compared to fair offers, and more so in the second half of the game. Interestingly, even fair offers seemed to have become more irritating in the second half of the game, pointing at the effect of the anger-infused social dynamics between participants and the putative proposers. In addition, we found a significant interaction between emotion clusters and gain-groups [$F_{(1,58)} = 5.72$, $p = 0.02$, $\eta_p^2 = 0.09$] suggesting that LGs reported enhanced anger (1.54 ± 1.11) compared to positive emotions (0.96 ± 0.67) [$p = 0.08$], while HGs did not differ between these emotion clusters [anger = 1.26 ± 1.14 ; positive = 1.45 ± 0.94 ; $p = 0.82$]. There were no differences between LGs and HGs in each of these emotion clusters [$p_{\text{anger}} = 0.71$; $p_{\text{positive}} = 0.25$]. This indicates that while LGs are primarily angry, HGs seem to balance anger and positive emotions. To further examine this finding we incorporated both anger and positive clusters in a regression model and found that incorporating both emotional clusters explained significantly more than each of them alone [$R^2_{\text{anger}} = 0.07$, $p = 0.04$; $R^2_{\text{positive}} = 0.09$, $p = 0.02$; $R^2_{\text{both}} = 0.21$, $p = 0.001$, $R^2_{\text{change}} = 0.14$, $p = 0.003$]. We thus calculated a standardized emotional valence index (EVI) that incorporated both emotion clusters: (positive cluster - anger cluster) / (positive cluster + anger cluster). A positive EVI indicated that more positive and less anger emotions were reported while a negative EVI indicated the reverse. As expected, a more positive EVI was related to greater total gain [$r = 0.44$, $p < 0.001$; Fig. 1D]. These results suggest that as subjects gained more money they reported less anger, which is in line with our hypothesis, but also more positive emotions.

Skin conductance

Averaged SCR intensity and latency, for the two fairness categories (fair/unfair) were submitted separately to an ANOVA with gain-groups (LGs/HGs) as between-subject factor. In line with our hypothesis, we found a gain-groups main effect in SCR-latency [$F_{1,35} = 6.40$, $p = 0.02$, $\eta_p^2 = 0.15$], such that HGs had slower SCR (2401.52 ± 373.54 ms) compared to LGs (2834.08 ± 425.55 ms). In fact, there was a positive correlation between total-gain and SCR-latency [$r = 0.54$, $p = 0.001$]; Fig. 1E), indicating that slower SCR onsets related to increased gain in the game. No other significant results were found for SC measures (Inline Supplementary Table S4).

Inline Supplementary Table S4 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

¹ The average emotional rating for each of the 16 different emotions of the GEW for all periods and all rounds of the game were submitted to a repeated-measures ANOVA and a significant effect was found [$F_{15,885} = 15.25$, $p < 0.001$, $\eta_p^2 = 0.21$], indicating that Anger (1.86 ± 1.38) was the most dominant reported emotion [Tukey's $p < 0.05$, two-tailed], though just qualitatively higher in comparison to Hostility (1.59 ± 1.48) and Contempt (1.55 ± 1.55).

Gain-group differences emerge from within the dynamics of the modified-UG

If the above detailed differences between gain-groups reflected a priori predispositions unrelated to our interactive paradigm, then we might expect to see these differences already at the first round of the game. We thus submitted acceptance rates of the first offer to a 2 (fairness: fair/unfair) \times 2 (gain-groups: LGs/HGs) ANOVA and found no main effect of gain-groups [$F_{1,56} = 0.36$, $p = 0.55$, $\eta_p^2 = 0.01$] and no interaction effect [$F_{1,56} = 1.93$, $p = 0.17$, $\eta_p^2 = 0.03$]. There was no difference even when considering only the subset of first unfair-offers [$t_{28} = 0.47$, $p = 0.64$, *Cohen's d* = 0.17]. We next submitted EVI of the first offer to a similar analysis and found no main effect of gain-groups [$F_{1,56} = 0.02$, $p = 0.88$, $\eta_p^2 = 0.00$] and no interaction effect [$F_{1,56} = 0.05$, $p = 0.83$, $\eta_p^2 = 0.00$] and no difference even when considering only anger or only positive ratings for the subset of first unfair-offers [anger: $t_{29} = -0.86$, $p = 0.40$, *Cohen's d* = 0.31; positive: $t_{29} = 0.55$, $p = 0.58$, *Cohen's d* = 0.20]. In addition, there was no difference in sympathetic arousal in the first offer as measured by SCR intensity and latency (see methods above). Therefore, the differences found between gain-groups seem to emerge from within the dynamics of our modified-UG.

Brain activity

To investigate the neural substrates of high vs. low total-gain in our modified-UG we first examined the gain-groups main effect (Inline Supplementary Table S5) which revealed, as expected, increased activity in an anterior region of the vmPFC, but unexpectedly, also decreased activity in the brainstem (BS), among HGs relative to LGs (Fig. 2A). We further found that increased BS activity correlated with faster SCR latencies [$r = -0.40$, $p = 0.02$; Fig. 2B]. In addition, a dissociated pattern of activation in the vmPFC and BS was found between gain-groups (LGs/HGs) and offers (fair/unfair) [$F_{1,52} = 5.70$, $p = 0.02$, $\eta_p^2 = 0.10$; Fig. 2C] such that during unfair offers HGs displayed increased vmPFC activity and decreased BS activity [$p < 0.001$], while LGs displayed the reverse pattern of activity [$p < 0.001$]. We did not find a correlation between BS activity and EVI [$r = -0.08$, $p = 0.55$]. Importantly, however, the positive relation between vmPFC activity and total-gain was partially mediated by the EVI (Fig. 2D). In other words, with increased vmPFC activity, more positive and less angry feelings were reported (higher EVI), and more gain was accumulated throughout the game.

Inline Supplementary Table S5 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

We next examined whether there would be differences in the neural correlates of unfair compared to fair offers with relation to the two gain-groups, and found that HGs exhibited increased activity in the dorsal posterior Insula (dpl) during unfair offers (Fig. 3A). There was no correlation between dpl activity and EVI [$r = 0.18$, $p = 0.20$], but there was a correlation with SCR-latency [$r = 0.40$, $p = 0.02$] (Fig. 3B), which supports dpl's involvement in the physiological experience attributed to unfair-offers. In addition, dpl and vmPFC activity during unfair offers was positively correlated [$r = 0.31$, $p = 0.02$; Fig. 3C], which might be indicative of dpl's involvement in accepting unfair offers.

Functional connectivity

A key aspect in the portrayal of an emotional experience is delineating the dynamic nature of its underlying neural manifestation (Raz et al., 2012). To further elucidate the neural dynamics of the modified-UG and to fully explore the relations between the vmPFC, BS and dpl and the entire brain, we next opted for task-dependant functional connectivity analysis using PPI. Using vmPFC, BS and dpl as seed regions in separate PPI analyses we observed no changes in connectivity related to total-gain when contrasting fair and unfair offers. We thus conducted additional analyses on unfair offers relative to baseline, but included as

covariate the specific gain accumulated during these unfair offers. We found a change in functional connectivity between the dpl and the medial thalamus (mT), and more so as gain increased (Fig. 4A; Inline Supplementary Table S6). In addition, the positive relation between dpl-mT connectivity during unfair offers and gain accumulated during these unfair offers was partially mediated by the subjective emotional experience specifically during the unfair offers (Fig. 4B).

Inline Supplementary Table S6 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

Taken together, it seems that two neural measures had a role in modulating the emotional experience during our modified-UG en route to increased gain. The first related to vmPFC activity throughout the entire game (all offers) and the second to dpl-mT connectivity during the more angering situations (unfair offers). To explore the relationship between these two measures and total-gain we conducted a regression analysis which showed that although vmPFC activity during the offer period better explained the variance in total-gain than dpl-mT connectivity during unfair offers, together they explained significantly more [$R^2_{\text{vmPFC}} = 0.30$, $p < 0.001$; $R^2_{\text{dpl-mT}} = 0.17$, $p = 0.002$; $R^2_{\text{both}} = 0.44$, $p < 0.001$; $R^2_{\text{change}} = 0.14$, $p < 0.001$]. This finding indicates that both these neural measures had a contribution in explaining variance in total-gain and suggested that they might reflect separate though related processes.

Discussion

By incorporating sequential on-line verbal negotiations with an obnoxious proposer intended to infuse anger in a repeated UG, we increased ecological validity, enhanced the emotional turmoil and thus created a naturalistic interpersonal conflict over monetary resources. This is supported by the findings that participants reported more anger than other emotions, especially during unfair offers, and more so at the second half of the game. Moreover, in line with our expectations, as participants gained more money, they reported less anger and more positive feelings, had slower decision reaction-times (Inline Supplementary Figure S2) and had slower sympathetic responses. These findings converge to indicate individual differences in emotional experience that relate to the final monetary outcome of the interpersonal conflict. Furthermore and as expected, participants who gained more money and also reported less anger showed increased activity in the vmPFC during the offer periods, but unexpectedly also decreased activity in a region of the BS. This opposite relationship between vmPFC and BS was more accentuated during unfair offers. Lastly, specifically during unfair offers, high-gain participants had increased dpl activity and dpl-mT connectivity. Strikingly, both vmPFC activity during all offers and dpl-mT connectivity during unfair offers modulated the subjective emotional experience as depicted by the emotional valence index, en route to a beneficial monetary outcome of the interpersonal conflict.

Inline Supplementary Fig. S2 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

The tendency to accept anger-infused UG-offers is typified by a balanced emotional profile

While the idiosyncratic emotional profiles capture variability in how participants managed the interpersonal conflict, the question remains whether HGs had a different emotional reactivity pattern or whether they actively engaged in emotion regulation. Indeed, there is an open debate as to whether generation and regulation of emotions are separable processes, or intertwined in one another (Gross and Barrett, 2011). However, it is generally acknowledged that emotions unfold over time, and congruently the *process model of emotion regulation* (Gross and Thompson, 2007) suggests that regulatory processes may intervene at any time during this temporal dynamics, even before emotional response tendencies. It is thus implied that a less reactive person may in fact engage, whether implicitly or explicitly, in some form of regulation.

Interestingly, similar to other studies implying spontaneous uninstructed emotion regulation (e.g., Drabant et al., 2009) we found no differences between gain-groups in trait measures related to emotional reactivity, such as Trait Anger or Anxiety, nor to Neuroticism. In fact, we did not find differences in any trait measure except for Agreeableness (Inline Supplementary Table S2), which is a personality measure generally related to pro-social orientation, but was also specifically associated with regulating anger and aggression during interpersonal conflict (Jensen-Campbell and Graziano, 2001; Meier et al., 2006). Taken together, we argue that a mental process with specific neural patterns emerged from within the dynamics of the interpersonal conflict and enabled HGs to end up with greater monetary outcome. In view of HGs' elevated Agreeableness scores, this might have involved recruiting pro-social thoughts as a means of self-regulation. Thus said, it does not mean that HGs were not angry at all, but as evident, they seemed to have balanced between anger and positive feelings. Such an emotional balance corresponds to the notion that psychologically resilient people, those people who are able to efficiently adapt themselves to changing situational demands and thus able to cope with stressful events, do so by enhancing positive as well as reducing negative emotions (Tugade and Fredrickson, 2007).

One may argue that strict strategic reasoning caused LGs to reject offers to improve their stance in subsequent negotiations (Slembeck, 1999). If that was the case, we wouldn't expect LGs to report increased anger and decreased positive emotions, rather a more stable, perhaps even indifferent emotional experience. In addition, predicting that some participants might opt for the use of such strategies, we provided our putative proposers with specific scripts to handle such demands (see Supplementary methods). Thus, even though strategic reasoning might have taken place at certain time-points along the game, it is unlikely that it determined the ample converging behavioral and physiological differences between gain-groups. On the other hand it is important to emphasize that since participants' decisions and negotiating skills did not have an actual influence on subsequent offers, though they were led to believe so, our results do not imply that HGs are better at strategic reasoning or better negotiators than LGs.

The neural substrates of the tendency to accept UG-offers modulate the emotional experience

As hypothesized, we found that the vmPFC had a major role in accepting UG-offers, supposedly by modulating the emotional experience, and in reflecting individual differences in managing interpersonal conflict beneficially. Nevertheless, in view of vmPFC's involvement in valuating reward (Rolls, 2004) and previous findings relating UG-behavior to reward sensitivity (e.g., Scheres and Sanfey, 2006), one might suggest that gain-groups differ in reward sensitivity. However, trait measures of sensitivity to reward and punishment, as well as a post-scan self-report of participants' desire to gain money in the game did not relate to vmPFC activity and did not differ between gain groups (Inline Supplementary Table S2). In fact, the only trait measure which did correlate with vmPFC activity was the habitual use of expressive suppression as an emotion regulation strategy (Inline Supplementary Table S2). Indeed, the vmPFC has been generally implicated in implicit emotion regulation (Phillips et al., 2008; Gyurak et al., 2011), and regulating anger and aggression in particular (Davidson et al., 2000). Notably, while functionalities such as reward processing have been commonly centered at rather posterior, subgenual regions of the vmPFC, we located a more anterior aspect of the vmPFC. This alludes to previous studies that associated different roles for anterior and posterior regions of the vmPFC in decision-making. It has been suggested that posterior-vmPFC encodes concrete/material rewards while anterior-vmPFC encodes long-term/abstract rewards (Rolls, 2004; Moretti et al., 2009). An alternative proposition was that posterior-vmPFC encodes decision values, the value of choosing to reject or accept an offer, while anterior-vmPFC encodes experienced values, the actual

reward or positive emotion in view of that decision (Baumgartner et al., 2011). However, these two alternatives seem to be in disagreement as decision values are relatively abstract while experienced values are rather concrete. From a different perspective, it is possible that we identified an anterior-vmPFC region because of its involvement in flexible adaptations to contingencies during dynamic decision-making (Boorman et al., 2009; Kovach et al., 2012). In other words, anterior-vmPFC seems to have a role in the ability to learn from on-going experiences and update behavior in a response-contingent manner. Interestingly, we found among HGs only that vmPFC activity increased between the 1st and 2nd half of the game extending to include both fair and unfair offers (Inline Supplementary Figure S3). Moreover, a recent meta-analysis of emotion regulation studies revealed a rather anterior aspect of the vmPFC involved in the extinction of a negative emotional responses to a previously conditioned stimulus (Diekhof et al., 2011). While speculative, this may suggest a flexible generalization in the application of an implicit process related to emotion regulation amongst HGs, especially since anger increased in the second half of the game for both fair and unfair offers.

Inline Supplementary Fig. S3 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

In addition to the vmPFC, we found an unexpected cluster of activation in the BS, which was stronger for LGs compared to HGs. This cluster seems to correspond to the anatomical location of the Locus Coeruleus (LC; Keren et al., 2009), a subcortical nucleus located in the dorso-rostral Pons and the major source for Noradrenalin in the brain, thus critically involved in arousal and stress response (Samuels and Szabadi, 2008a,b). Localizing the LC from BOLD fMRI has been debated (Astafiev et al., 2010; Minzenberg et al., 2010; Schmidt et al., 2010), yet the specific location of the BS activation cluster, the relation found between its' activity and sympathetic arousal as measured by SCR-latency, and the fact that the LC has been consistently and reliably involved in human aggression (Haden and Scarpa, 2007), together supports that the BS activity indeed corresponds to the LC region. Interestingly, the inverse relationship found between vmPFC and BS/LC suggests that the vmPFC might have had a role in attenuating arousal-related brain activity. In support, a marginally significant mediation model (Inline Supplementary Figure S4) pointed that increased vmPFC activity might be involved in slower SCR latencies by supposedly diminishing BS/LC activity.

Inline Supplementary Fig. S4 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

The dpl was another unexpected cluster of activation, which during unfair offers was stronger for HGs compared to LGs and also positively related to both SCR-Latency and vmPFC activity. The dpl, through its anatomical connection to the medial-Thalamus, which continues the pathway to the brainstem and finally to the spinal cord, is regarded as the primary region of interoception, that is attending to and representing the internal physiological state of the body (Craig, 2002; 2011). The neural-coupling that we found between dpl and mT corresponds to this anatomical pathway and contributes to accepting unfair offers by supposedly modulating the emotional experience, specifically during the more angering offers. Similarly, a recent study found that interoceptive awareness was related to UG behavior, moderating the relationship between skin-conductance and acceptance rates (Dunn et al., 2012), however an attempt to determine the link between interoceptive awareness and emotion regulation in regards to UG-behavior was inconclusive (van't Wout et al., 2013). Interestingly, a study on experienced mindfulness meditators, considered to recruit emotion regulation through their practice of non-judgmental acceptance of internal and external experiences, found that they had higher acceptance rates and higher dpl activity compared to controls (Kirk et al., 2011). Consistently, our results may suggest that dpl has a direct role in modulating the emotional experience during such volatile situations as unfair UG-offers, thus supporting theories of emotion which emphasize bodily feedback via interoceptive processing (Bechara et al., 2000; Craig, 2011).

The importance of naturalistic settings for neuroscience

In the current study, within the confined environment of the MRI scanner, we infused genuine interpersonal anger to a social decision-making task by embedding on-line spontaneous verbal interactions as a negotiation phase after each ultimatum-offer. Importantly, we separated between a controlled and easily modeled period for analysis (the offer period) and an uncontrolled interactive period for the induction of an emotional experience (the negotiation period). We found a strong relationship in the subjective emotional experience during these two periods and that there was no difference in the intensity of this experience between the two periods. Congruent with the dynamics of interpersonal conflict, this may suggest that the negotiation periods and the actual offers made intermingled in inducing the overall emotional experience. Our study design did not enable us to draw conclusions as to what neural processes engage during the actual interactions and we did not design it to directly compare the effects of having such interactions compared to a standard UG. This provides a promising path for future studies. Yet the increased ecological validity of the decision-making process and of the emotional experience alludes to the significance of our findings to real-life situations. Moreover, the vmPFC and dpl findings replicate previous findings, while we may speculate that the BS/LC finding is related to our ecologically valid anger-infused manipulation since it was not previously reported in the UG-context. We thus support recent conceptual developments in shifting neuroscientific endeavor, especially in the neuroscience of affect, from an “isolated” to a “socially interacting” brain mode (Przyrembel et al., 2012; Schilbach et al., 2013).

Concluding remarks

The current study's findings point towards two possible processes that underlay the ability to reach a beneficial outcome to interpersonal conflict, possibly by modulating the emotional experience evoked during this kind of dispute. The primary process of this suggested mechanism is centered on the vmPFC and seems to be activated throughout the entire interaction, and might also have a role in attenuating BS/LC-related arousal. The secondary process is centered on the dpl and is particularly involved during the more volatile moments of the interaction. Results indicate that recruiting both processes is most effective for a beneficial outcome. These findings are particularly compelling as they relate to neural activity measured before the actual decision to accept or reject an offer has been made. Moreover, since our paradigm enabled participants to spontaneously experience emotions during dynamic naturalistic social interactions, findings relate to everyday life in which emotion regulation is engaged spontaneously (Gross and Thompson, 2007). Thus said, our paradigm is limited both in power due to its' ecological nature, and by our analysis which was focused on individual differences. These two methodological features could have determined the regions depicted by our whole-brain analysis. Indeed, others who utilized a more standardized version of the UG have found executive-function and emotion-reactivity related brain regions (e.g., Sanfey et al., 2003). We did not employ as control task such a standard single-shot UG and thus it is unknown to what degree our own results generalize to previous UG literature. Nevertheless, we suggest that the converging results from behavioral, physiological and neural measures point to a multi-level mechanism that seems to be related to an implicit and spontaneous process of anger regulation, and might also increase the chances for cooperation rather than conflict escalation. Interestingly, our findings indicate that such a process of emotion regulation consists of balancing both anger and positive feelings. Future research should scrutinize and generalize our findings to the population at large, by increasing the heterogeneity of the participants, such as comparing both genders and having a larger range of ages. In furtherance, open questions remain such as when and how people recruit the suggested processes, if and how do these processes interact and whether

they represent an innate or an acquired tendency. Future studies could also investigate the relevance of these processes to individually tailored interventions focused on emotionally balanced pro-social interactions.

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Conflict of interest

The authors declare that there are no competing financial interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.07.003>.

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