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Social stress enhances intuitive prosocial behavior in males while disrupting self-reward processing: Evidence from behavioral, computational, and neuroimaging studies

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ABSTRACT

In this study, we present behavioral, computational, and neuroimaging evidence that social stress enhances intuitive prosocial value processing while impairing self-reward processing. When deciding on monetary rewards for individuals at various social distances, participants who exhibited elevated cortisol levels following a social stress task were more inclined to choose a disadvantageous unequal option. Neuroimaging data revealed that participants more likely to choose the disadvantageous unequal option exhibited increased encoding of other-regarding rewards in the ventral medial prefrontal cortex (mPFC), whereas the dorsal mPFC exhibited a decrease in encoding. Mediation analyses further indicated that both the ventral and dorsal mPFC indirectly mediated the relationship between heightened cortisol levels and a greater likelihood of choosing a disadvantageous unequal option. Additionally, effective connectivity analysis results demonstrated that cortisol has an excitatory effect on the dorsal mPFC via the ventral striatum, while simultaneously sending inhibitory signals to the dorsal mPFC via the dorsal striatum. These findings provide empirical evidence to clarify the ambiguity surrounding the effects of stress on prosocial decision-making, suggesting that social stress disrupts deliberative decision-making while simultaneously promoting intuitive prosocial motivation through the differential modulation of hierarchically organized cortico-striatal loops.

1. Introduction

Prosocial behavior is fundamental to human social life, fostering cooperation, trust, and psychological well-being across diverse interpersonal contexts (Fehr and Fischbacher, 2003; Tomasello, 2014). While such behavior often reflects deliberate moral reasoning or long-term social strategies, it can also emerge spontaneously, driven by emotional resonance or intuitive responses (Zaki and Mitchell, 2013). Yet, the expression of prosociality is not static; it is shaped by various contextual factors, one of the most influential being stress. Although stress is traditionally associated with threat-driven, self-preservative responses (Sapolsky, 2004), emerging evidence suggests that it can also promote affiliative behaviors, particularly in social contexts (von Dawans et al., 2012; Tomova et al., 2017; Margittai et al., 2015, 2018). This dual role of stress raises a critical question in social neuroscience: under what conditions does stress enhance or impair prosocial decision-making?

The complexity of this relationship is well illustrated in the inconsistent behavioral findings across empirical studies. Some have reported that acute stress promotes helping and sharing behaviors (von Dawans et al., 2012; Margittai et al., 2015), while others found the opposite, with stress leading to increased selfishness or reduced generosity (Vinkers et al., 2013; Bendahan et al., 2017; Schweda et al., 2020). A recent meta-analysis by Nitschke et al. (2022) concluded that commonly assumed moderating variables such as stress induction method, participant sex, or time delays after stress exposure do not consistently explain these discrepancies. Instead, it appears that task design and the underlying cognitive and neural mechanisms may be more decisive in determining whether stress facilitates or hinders prosociality.

One compelling theoretical framework that attempts to reconcile these divergent findings is the “Tend-and-Befriend” theory, proposed by Taylor et al. (2000). This model suggests that stress, especially in

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affiliative or interdependent social species like humans, may trigger affiliative responses rather than just fight-or-flight tendencies. Tend-and-Befriend posits that, in the face of stress, individuals—particularly females—may exhibit increased caregiving and social bonding behaviors as an adaptive strategy for managing threat and ensuring group cohesion. This perspective broadens the conventional view of stress and highlights the potential for prosocial behavior to emerge not in spite of stress, but because of it.

However, the neural mechanisms that underlie these stress-induced shifts toward prosociality remain largely unexplored. Neuroimaging studies have only recently begun to examine how acute stress influences value-based social decision-making. For instance, Schulreich et al. (2022) found that increased cortisol levels reduced charitable donations in individuals with high mentalizing capacity, a change mediated by decreased activity in the dorsolateral prefrontal cortex (dlPFC). Similarly, Forbes et al. (2024) showed that stress led to fewer prosocial choices in low-effort situations, accompanied by reduced sensitivity in the dorsal anterior cingulate cortex (dACC) to other-regarding values. These findings suggest that stress impairs deliberative cognitive control and effort valuation systems, resulting in less generous behavior—at least under certain task configurations.

An alternative possibility, however, is that prosocial behaviors may not always require cognitive control. Yu (2016) proposed that stress shifts decision-making away from deliberative, prefrontal processes and toward intuitive, subcortical systems. From this perspective, stress may not simply suppress prosociality, but rather alter the balance between deliberative and intuitive modes of decision-making. In situations where prosocial behavior is the intuitive or emotionally salient response, stress might actually enhance generosity. This hypothesis aligns with the idea that helping others can be a reflexive reaction under emotional arousal (Zaki and Mitchell, 2013), and that self-oriented choices sometimes require more cognitive deliberation (Krajbich et al., 2015). Thus, the behavioral consequences of stress may depend less on whether prosocial behavior is inherently “good” or “bad,” and more on whether it is cognitively effortful or intuitive in a given context.

To investigate this possibility, it is essential to consider the functional architecture of the medial prefrontal cortex (mPFC), a key region involved in value-based decision-making (O’Doherty et al., 2004; Kable and Glimcher, 2007; Rushworth et al., 2012). The mPFC is functionally heterogeneous, comprising subregions such as the ventromedial PFC (vmPFC), dorsomedial PFC (dmPFC), and rostromedial PFC (rmPFC), each of which supports distinct computational processes (Kim, 2020; Klein-Flugge et al., 2022; Lieberman et al., 2019). The vmPFC is implicated in representing subjective value and integrating information about social rewards and prosocial motivations (Kringelbach, 2005; Strombach et al., 2015; Zaki and Mitchell, 2013; Ruff and Fehr, 2014). In contrast, the dmPFC is associated with more abstract, deliberative computations, such as weighing future consequences, integrating contextual information, and inferring others’ intentions (Hasz and Redish, 2020; Domenech et al., 2020; Piva et al., 2019; Wittmann et al., 2016). These subregions are embedded in distinct cortico-striato-thalamic loops (Haber, 2016): the vmPFC interacts with the ventral striatum (VS) to support emotionally driven, intuitive valuations (Bouret and Richmond, 2010), while the dmPFC interacts with the dorsal striatum (DS) to support goal-directed, cognitively demanding decisions (De Kloet et al., 2021; Smith et al., 2019).

Crucially, stress hormones such as cortisol have been shown to selectively modulate these circuits, suppressing activity in prefrontal regions like the dmPFC while enhancing subcortical responsivity (Ironside et al., 2018; Vogel et al., 2017), thereby biasing decisions toward more intuitive or habitual modes. If prosocial behaviors are represented within vmPFC-VS circuits and can emerge through intuitive valuation, stress may enhance generosity in situations where deliberation would otherwise introduce self-interest. Conversely, when generosity requires abstract reasoning or integration of complex contextual cues, as supported by the dmPFC-DS loop, stress may reduce prosociality by impairing these capacities.

One paradigm particularly well-suited for testing this dual-process account is the social discounting task, which requires participants to choose between monetary rewards for themselves and for others at varying social distances (Jones and Rachlin, 2006). The task captures the trade-off between selfish and prosocial motivations and has been consistently linked to activity in the vmPFC and VS during generous choices (Strombach et al., 2015; Hill et al., 2017; Soutschek et al., 2017; Ou et al., 2021). Previous behavioral studies have shown that stress increases generosity toward close others while reducing it toward distant others (Margittai et al., 2015; Schweda et al., 2020), suggesting that stress interacts with emotional proximity in shaping social preferences. Moreover, pharmacological evidence suggests that dopaminergic modulation plays a central role in prosocial motivation, as blocking D2 receptors eliminated sex differences in generosity in the social discounting task (Soutschek et al., 2017).

To address this gap, the present study used a modified version of the social discounting task that included a disadvantageous unequal condition, in which participants could choose to give more money to another person than to themselves. This addition allowed us to examine self-sacrificing forms of prosociality in explicitly disadvantageous contexts. Building on previous findings that acute stress can increase such behaviors in male participants (Margittai et al., 2015, 2018), we aimed to replicate and extend this effect while identifying the neural substrates involved. Specifically, we hypothesized that cortisol responses would be associated with increased generosity, mediated by greater activation in the vmPFC. Additionally, we predicted that stress would impair the function of the dmPFC, reducing the integration of contextual information such as social distance, and thereby promoting intuitive prosocial choices in the unequal condition.

By combining behavioral, endocrinological, and neuroimaging measures, this study seeks to elucidate how stress reconfigures the neural computation of value in social decisions. In doing so, it offers a mechanistic account of when and how stress may facilitate prosociality—particularly when generosity becomes the path of least resistance in the mind.

2. Materials and method

2.1. Participants

49 healthy male participants (mean ± standard deviation = 25.3 ± 2.39) were recruited for the study. Participants with a history of psychiatric conditions, current medication use, or claustrophobia were excluded from the study. Participants were instructed the day before the experiment to abstain from alcohol and ensure adequate sleep. On the day of the experiment, they were asked to refrain from eating, consuming caffeinated beverages, or smoking for at least two hours before the start. This study was conducted between 1:00 pm. and 6:00 pm. to minimize the impact of circadian rhythms on cortisol levels. Only male participants were included because previous research suggested that hormonal stress responses in females could vary with menstrual cycle phase (Kirschbaum et al., 1999). Eight participants were excluded from the analysis due to excessive head movement ($N = 2$), a misunderstanding of the task ($N = 1$), or a lack of belief in the money-sharing manipulation ($N = 5$). All participants were fully informed about the experimental procedures and provided written consent before scanning. The study was approved by the Korea University Institutional Review Board, and participants received monetary compensation of approximately ₩45,000 (about $40) for their participation.

2.2. Experimental procedures

Upon arrival, participants provided their first saliva sample (T1), followed by completing the Positive Affective Negative Affective Scale (PANAS) and a series of questionnaires assessing individual differences.

These included the Behavioral Inhibition/Activation Scale (BIS/BAS), the Revised Morningness-Eveningness Questionnaire (rMEQ), the Trier Inventory for Chronic Stress (TICS), the Social Desirability Scale (SDS), the Trait Scale of the State-Trait Anxiety Inventory (STAI), personality traits, and the Levenson Self-Report Psychopathy Scale (LSRP). Participants then received detailed instructions for the Montreal Imaging Stress Task (MIST) and the social discounting task, and completed practice trials to ensure a full understanding of each task. Before entering the scanner, participants provided a second saliva sample (T2) and listed the names of their acquaintances corresponding to four social distances (i.e., 1, 5, 10, 20), which were used in the social discounting task. Following this, participants were escorted to the scanning room. Participants were instructed to lie still in a comfortable position while a 9-minute resting-state fMRI scan (preRSFC) was conducted. Following this, participants performed the MIST inside the scanner for 10 min, although MRI data were not acquired during this task. Immediately after the MIST, a second resting-state fMRI scan (postRSFC) was conducted for 9 min. Upon completion, participants provided a third saliva sample (T3) and then proceeded with the social discounting task, which was followed by structural MRI image acquisition. After leaving the scanning room, participants provided a fourth saliva sample (T4) and completed a post-experiment survey.

2.2.1. Social discounting task

Before entering the scanning room, participants received both verbal and written instructions for the social discounting task and completed practice trials to ensure full comprehension. They were then asked to assign a name (i.e., target) to each designated social distance (SD): SD 1 for the closest friend, SD 5 for a close friend, SD 10 for a friend, and SD 20 for an acquaintance. Participants were explicitly instructed to provide names of friends only, excluding relatives or family members. For SD 50, the recipient was defined as a person from the same university campus, and for SD 100, a complete stranger. Participants' understanding of the task was verified through a verbal quiz. To enhance task immersion regarding monetary sharing behavior, participants were informed that they would be asked to provide contact information for the individuals they listed, so that monetary incentives could be delivered after the experiment.

A modified version of the social discounting task (Strombach et al., 2015) was implemented, in which participants chose between a monetary incentive for themselves or a money-sharing decision with a target at a specific social distance (Fig. 1A). In the "equal condition," a generous decision meant allocating an equal amount of ₩20,000 (about $18) to both the participant and the target. Five different levels of monetary incentives for participant (₩19,000, ₩25,000, ₩31,000, ₩37,000, ₩43,000) were presented for comparison against the prosocial decision. For display purposes, three zeros were omitted from the monetary values during the experiment. For example, in an "equal condition" trial, participants would choose between keeping "43" (₩43,000; approximately $40) for themselves or receiving "20" (₩20,000; approximately $18) each for both themselves and the designated target.

Additionally, a "disadvantageous unequal condition" was included, where the target received more money than the participant (e.g., target: 30 and self: 10) if a generous decision was made. This self-sacrificing condition was incorporated because previous studies reported that stressed males tended to allocate a larger portion of their endowment,

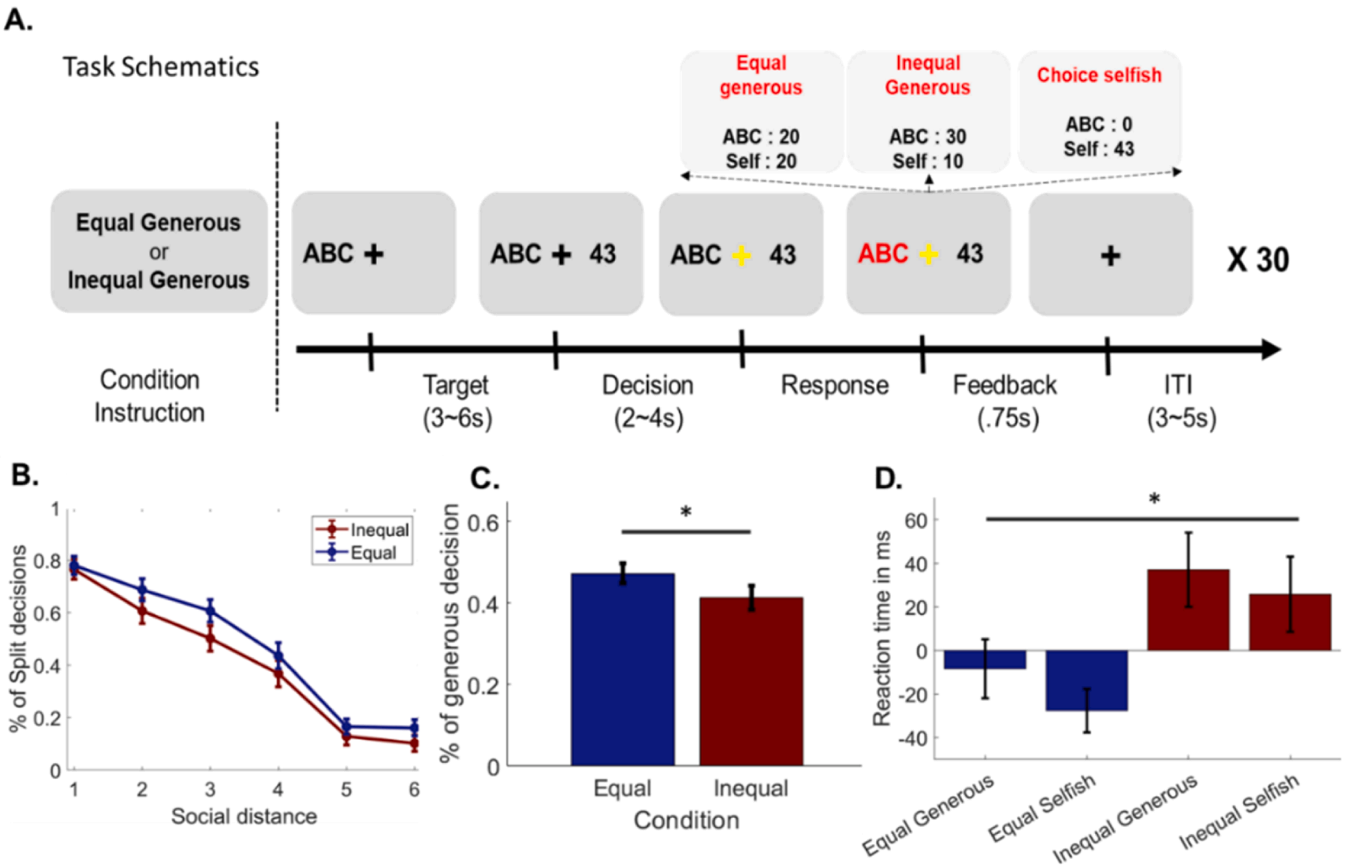

Fig. 1. Experimental design and results. (A) Schematic of the task design. In each trial, a target at varying social distances was presented, followed by an incentive amount for the self. Choosing the target's name (e.g., ABC) would indicate a generous decision, resulting in a payoff of 20 for both the self and the target in the equal condition, or 30 for the target and 10 for the self in the unequal condition. (B) The average rate of generous decisions varies significantly across social distances. (C) When aggregated across social distances, the difference in generosity between the two conditions remains significant. (D) The participants responded faster in the equal condition than in the unequal condition, regardless of the decision made. $^{*}p < 0.05$ for all statistical analyses.

especially to socially close targets, compared to themselves (Margittai et al., 2015; Margittai et al., 2018). The equal and unequal conditions were presented in a pseudorandom order. At the start of the experiment and every 30 trials thereafter, information about the condition and detailed instructions for each payoff were displayed.

During each trial, participants first viewed the recipient's name displayed for the money-sharing decision (target phase, 3–6 s; see Fig. 1A). Next, the incentive amount for the participant was displayed next to the target's name for 2–4 s (option phase). The fixation point color in the middle of the screen then changed to yellow, signaling participants to select their preferred option (decision phase). The option phase and decision phases were separated to distinguish the value computation process of the money-sharing decision from the motor-related decision process. Following participants' selections, feedback was provided for 0.75 s, followed by an inter-trial interval (ITI) of 3–5 s. Optimal jittering between each phase was calculated using the software optSeq2 (Dale, 1999). The experiment lasted approximately 25 min and comprised 120 trials.

2.2.2. *Post-experiment survey*

In the post-experiment survey, participants rated their preference for each target using a sliding bar from 1 (most preferred) to 100 (least preferred). These preference ratings were later used as social distance based on preference information ($\mathrm{SD}_{\mathrm{pref}}$) in computational modeling and neuroimaging analysis. After completing the task, participants were asked whether they believed in the task manipulation and explained their rationale behind making selfish or generous decisions. Additionally, participants were asked whether they would send money to a specific social distance target or keep the money for themselves. Participants who did not believe that incentives would be sent to their designated targets after the experiment were excluded from the data analysis.

2.2.3. *Stress treatment and physiological measures*

To induce a psychological stress response, we employed the Montreal Imaging Stress Task (MIST; Dedovic et al., 2005), a widely used MRI-compatible stress elicitation task in social neuroscience research. The MIST treatment condition consisted of five arithmetic questions of varying difficulty levels, each lasting two minutes. Participants were required to solve these questions under time pressure while receiving both visual and verbal negative socio-evaluative feedback for incorrect answers or timeouts. After each difficulty level, participants' performance (i.e., accuracy) was monitored, and they received additional negative social-evaluative feedback (e.g., "You performed worse than the previous participant."). Participants were thoroughly instructed on the MIST and given sufficient practice before entering the scanning room.

To quantify stress reactivity of participants, we collected saliva samples four times throughout the experiment using a passive drooling procedure with a saliva collection aid kit (Part #: 5016.04) (**Supplementary Fig. S1**). We used saliva samples to measure physiological stress levels of individuals. Additionally, participants completed the Korean version of Positive and Negative Affective Scale (PANAS) immediately after each saliva sampling to measure their psychological stress levels. The collected samples were immediately stored at −20°C and later analyzed using a commercial immunoassay kit (Salimetrics, Cat. No. 1–3002). PANAS scores were analyzed separately for positive and negative affect.

To minimize confusion regarding terminology, we refer to the cortisol concentration level at T3 as "CORT," and "stress reactivity" as the change in cortisol levels from baseline (T1) to post-stress (T3). To investigate the influence of cortisol on social decision-making processes, we included either stress reactivity or CORT as a covariate in the neuroimaging general linear model (GLM) analyses as well as in the effective connectivity analyses (i.e., DCM-PEB analysis). All saliva samples were discarded after the immunoassay was completed.

2.3. *Behavioral data analyses*

2.3.1. *ANOVA and correlational analyses*

To assess the main effects of social distance and condition on prosocial decision-making, we conducted a two-way analysis of variance (ANOVA). The independent variables were social distance (1, 5, 10, 20, 50, and 100) and condition (equal and unequal), and the dependent variables were prosocial decision frequency and reaction time. Prosocial decision frequency was defined as the ratio of generous decisions to the total number of trials for a specific target and condition. We applied min-max normalization to the prosocial decision frequency for each participant across all social distances and summed the normalized frequencies for each condition, resulting in condition-wise frequency values ranging from 0 (no monetary split) to 6 (monetary split for all trials). This normalization aimed to evaluate individual prosocial decisions across social distances while reducing the impact of general prosocial tendencies.

We performed Pearson's correlation analyses to examine the association between computational parameter estimates and condition-wise prosocial decision frequencies. Additionally, Spearman's rank-order correlation was used to investigate the relationships between cortisol concentration and computational parameter estimates. Statistical analyses of the behavioral data were performed using IBM SPSS Statistics for Windows, version 26.0, while correlation analyses and data visualization were conducted using Python (3.9.7) with the Scipy (1.8.0) and seaborn (0.11.2) packages.

2.3.2. *Computational modeling analyses*

To explore the impact of different motivational factors on the modified social discounting task, we conducted a hierarchical Bayesian analysis using the hBayesDM package (Ahn et al., 2017) in R (version 4.1.0) with Stan (version 2.21.2). We modeled the subjective value of generous choices using 8 variations of hyperbolic or exponential functions of social distance (or preference-based distance), incorporating parameters that capture individual differences in self-reward sensitivity (β), inequality aversion (ρ), and social discounting sensitivity (k). Among the eight models tested, the best-fitting model included parameters for disadvantageous inequality aversion, self-reward sensitivity, and social discounting sensitivity, and was based on preference-based rather than social distance. This model outperformed all others, including the original social discounting model (Jones and Rachlin, 2006). Parameter estimation was conducted using hierarchical Bayesian parameter estimation with Hamiltonian Monte Carlo sampling. The best fitting model was selected based on the lowest leave-one-out information criterion (LOOIC), and the robustness of parameter estimates was validated through parameter recovery simulations. For a full decription of the computational modeling procedures, including model implementation, comparison, and parameter recovery, please refer to the Materials and Methods section in *Supplementary Material*.

2.4. *Neuroimaging data analyses*

2.4.1. *Functional neuroimaging acquisition and preprocessing*

Functional and structural neuroimaging data were collected using a 3T Siemens Trio MRI scanner (MAGNETOM Trio, A Tim System; Siemens AG, Erlangen, Germany) with a 12-channel birdcage head coil located at the Korea University Brain Imaging Center (KUBIC). T2*-weighted functional images were acquired using gradient echo-planar imaging (EPI) with Blood Oxygenation Level Dependent contrast (TR = 2000 ms; TE = 30 ms; flip angle = 90°; FOV= 240 mm; 3 × 3 × 3 mm in-plane resolution; 80 × 80 matrix size; and 36 slices with 3 mm gap). High-resolution structural images were also obtained (TR = 1900 ms; TE = 2.52 ms; flip angle = 9°; 1 × 1 × 1 mm in-plane resolution; and 256 × 256 matrix size).

The experimental task was presented via an MR-compatible LCD monitor mounted on the head coil (refresh rate: 60 Hz; display resolution: 800 × 600 pixels; viewing angle: 30°) using MATLAB 2020b and Cogent 2000 stimulus presentation software. Preprocessing of the neuroimaging data for social discounting task was conducted using the default settings of the CONN toolbox 2021b (www.nitrc.org/projects/com, RRID:SCR_009550). Preprocessing steps included realignment, distortion correction, centering to (0, 0, 0) coordinates, and slice-time correction in sequential order. The images were then spatially normalized to the standard Montreal Neurological Institute (MNI) EPI template and resampled to a voxel size of 2 × 2 × 2 mm. Finally, all processed images were smoothed with an 8 mm full-width at half-maximum (FWHM) Gaussian kernel.

2.4.2. First-level analyses

We investigated the neural substrates involved in the value computation process for generous decisions during the social discounting task. Specifically, we focused on brain regions that tracked trial-by-trial changes in subjective value for generous decision (SV_g) throughout the task. For this purpose, we constructed GLM1, which included: 1) an onset regressor for the target phase, 2) a parametric modulator representing social distance based on preference information (SD_{pref}) at the target phase, 3) an onset regressor at the option phase, and 4) a parametric modulator encoding SV_g at the onset of the option phase. Two additional analyses were conducted in which the parametric modulator SV_g was replaced by V_{other} and V_{self} (GLM1a and GLM1b, respectively; see **Table S7** for a summary of these GLM analyses).

To assess differential neural responses to SV_g under equal and unequal conditions, we constructed GLM2, consisting of: 1) an onset regressor at the target phase, 2) SD_{pref} as a parametric modulator, 3) an onset regressor for the equal condition, 4) SV_g as a parametric modulator for the equal condition, 5) an onset regressor for the unequal condition, and 6) SV_g as a parametric modulator for the unequal condition.

To further investigate neural responses associated with self-reward and social distance based on preference under equal and unequal conditions, we implemented GLM3, which included the same onset regressors as GLM2 but replaced the parametric modulators SV_g with $Amount_{self}$ and SD_{pref} (see Table S8 for a summary of the GLM analyses). GLM2 and GLM3 were estimated separately to mitigate potential multicollinearity between SV_g and SD_{pref}, which could lead to inflated beta estimates in GLM analysis (Mumford et al., 2015). This approach allowed us to independently examine neural correlates of overall decision value of generous decisions and its distinct subcomponents.

To explore neural responses associated with self-regarding value (V_{self}) during generous and selfish decisions, we constructed GLM4, which included:1) an onset regressor at the target phase, 2) SD_{pref} as a parametric modulator to capture variations in value, 3) an onset regressor for generous decisions, 4) V_{self} as a parametric modulator during generous decisions, 5) an onset regressor for selfish decisions, and 6) V_{self} as a parametric modulator during selfish decisions. To identify neural regions associated with inequality aversion in self-related reward processing, we performed a multiple regression analysis on the parametric modulation (i.e., V_{self}) contrast map for selfish vs. generous decisions. Individual differences in inequality aversion, social discounting sensitivity, and self-reward sensitivity were included as predictors to explain variance in V_{self}-related neural responses.

Six additional head motion regressors were included in all GLMs to correct for movement-related effects.

2.4.3. Second-level analyses

The primary objective of this study was to identify neural representations linked to behavioral discrepancies between unequal and equal conditions. These discrepancies were reflected in individual covariates of the inequality aversion parameter and cortisol concentration levels. To investigate the effects of stress on hierarchical value processing in the mPFC (Kim, 2020), we constrained our region-of-interest analyses using an mPFC mask (de la Vega et al., 2016). The Automated Anatomical Label (AAL) atlas (Tzourio-Mazoyer et al., 2002) without the cerebellum was used for whole-brain analyses.

We initially focused on the neural correlates of individual differences in disadvantageous inequality aversion. A second-level multiple regression was performed on the parametric modulation maps of SV_g and $Amount_{self}$ from GLM3, and SD_{pref} from GLM4 to identify neural regions whose activity correlated with inequality aversion parameters, whiling controlling for discounting and self-reward sensitivity as second-level covariates. We then examined correlations between cortisol concentration levels and neural responses to SV_g, $Amount_{self}$, and SD_{pref}, controlling for both inequality aversion parameter and stress reactivity.

Finally, we searched for brain regions reflecting group-averaged trial-by-trial changes in SV_g, $Amount_{self}$, and SD_{pref}, reporting activations surviving family-wise error correction at the peak voxel level (FWE*p*), with a threshold of $p < 0.05$. In addition, whole-brain exploratory analyses across all GLMs were conducted, identifying neural regions that survived multiple comparisons correction at the cluster level (FWEc $p < 0.05$). In summary, GLM1 investigated neural regions reflecting group-averaged processing of decision values (SV_g), other-regarding value (V_{other}), and self-regarding value (V_{self}), regardless of individual differences in generous behaviors. GLM2 and GLM3 focused on neural regions associated with individual differences in generous decisions between equal and unequal conditions, as represented by inequality aversion (See Table S9 for a summary of the results).

2.4.4. Mediation analysis

To examine the mediating role of identified neural regions in cortisol-related changes under unequal and equal conditions, we performed mediation analyses using the SPSS Process Macro version 4.1 (14). The model included cortisol concentration (CORT) as the independent variable, the inequality aversion parameter as the dependent variable, and parametric estimates from the dmPFC—associated with $Amount_{self}$—as the mediating variable. A parallel mediation model was tested with parameter estimates from the vmPFC, which reflected trial-by-trial changes in SD_{pref} and SV_g. Parametric estimates from the dmPFC and vmPFC were extracted as time-course averages from the peak-voxel, using MarsBaR software (Version 0.45) implemented in SPM12.

2.4.5. Dynamic causal modeling and parametric empirical Bayes

Neural investigations into inequality aversion have identified the vmPFC, dmPFC, and caudate as key regions underlying individual differences in generous and selfish behaviors. Notably, activity in the vmPFC and dmPFC are found to be modulated by cortisol in relation to inequality aversion. We observed that the bilateral caudate encoded V_{self} with increased sensitivity during selfish decisions as inequality aversion levels increased. This finding suggests that the caudate plays a crucial role in representing individual differences in the motivation for self-regarding decisions. The caudate is known to be critically involved in prosocial decision-making (Sul et al., 2015; Soutschek et al., 2017), and its signaling to the mPFC can be modulated by cortisol levels (Ironside et al., 2018). Based on these findings, we hypothesized that cortisol modulates signaling from the caudate to the mPFC, thereby influencing the balance between self-regarding and other-regarding value computations.

To test our hypothesis regarding the influence of cortisol on neural communication between brain regions involved in generous and selfish decisions, we conducted an effective connectivity analysis using SPM12. We employed dynamic causal modeling (DCM) to estimate the directionality and strength of neural signaling between predefined networks of brain regions (Friston et al., 2003). To examine group-level effects, we utilized parametric empirical Bayes (PEB), which integrates individual DCMs with covariates for each subject (Friston et al., 2016) The PEB analysis assesses the credibility of each connectivity and the effects of the covariates using a Bayesian framework (see Zeidman et al., 2019a, 2019b for detailed descriptions of DCM and PEB).

We selected peak voxels from four brain regions for our analysis: the dmPFC (Montreal Neurological Institute [MNI] coordinates: $x = -9$, $y = 30$, $z = 50$), vmPFC (MNI: $x = 10$, $y = 50$, $z = -8$), DS (MNI: $x = 16$, $y = 20$, $z = 10$), and VS (MNI: $x = -14$, $y = 24$, $z = 0$). The striatal ROIs (DS and VS) were chosen based on their positive correlation with inequality aversion and self-regarding value during selfish decisions (Table S5). The mPFC was included due to its mediating role in the relationship between inequality aversion and CORT levels (see Fig. 5C and 5D for the vmPFC and dmPFC, respectively). To refine the dmPFC ROI, we identified overlapping regions associated with CORT-related effects and generous value signals (SV_g), isolating key nodes involved in value computation for generous behavior (**Fig. S6, Table S9**). A 2 mm sphere time series was extracted from each region, adjusted using F-contrast, and entered into a full DCM model tailored to the task-related DCM analysis specifications.

For the PEB specification, we combined the full DCM models of individual participants to generate a single PEB model. This model included covariates for CORT, inequality aversion, and cortisol reactivity, allowing us to compute the group-level posterior predictive distribution for each connectivity under different conditions. We evaluated the probability of mean differences between conditions to determine whether cortisol levels influenced modulatory connectivity during generous versus selfish decisions. A two-tailed threshold of Bayesian contrast was set at $p < 0.05$.

3. Results

3.1. Behavioral results

Participants ($N = 41$) were less generous in the unequal condition than in the equal condition ($F(1, 40) = 7.05$; $p = 0.011$) and showed decreased generosity as social distance increased ($F(5, 36) = 36.80$; $p < 0.001$, Fig. 1B, 1C). Reaction time analysis revealed that participants responded faster in the equal condition, regardless of generosity, $F(40,1) = 5.392$; $p = 0.025$ (Fig. 1D). Again, participants responded faster in the equal versus unequal conditions across all social distance levels ($F(40,1) = 6.355$; $p = 0.016$, **Fig. S2**). Participants reported changes in positive and negative affect throughout the experiment. Positive PANAS scores decreased over time ($F(3, 38) = 7.265, p = 0.001$), while negative scores increased ($F(3,38) = 5.722$, $p = 0.002$). Bonferroni post-hoc analysis comparing PANAS scores before and after the stressor with an adjusted alpha level of 0.0125 per test (0.05/4) indicated a significant decrease in positive affect from T2 ($M = 27.54$, $SD = 7.81$) to T3 ($M = 26.05$, $SD = 7.37$) and an increase in negative affect from T2 ($M = 16.36$, $SD = 8.11$) to T3 ($M = 18.61$, $SD = 7.16$). A repeated-measure MANOVA of saliva samples across four time points indicated a significant main effect ($F(3, 38) = 3.346$), $p = 0.029$) of time. Bonferroni-adjusted pairwise comparisons of six possible combinations among four time points indicated a significant drop in cortisol levels from T3 to T4 (adjusted $p = 0.027$). The difference in cortisol concentration level from the baseline indicated significant changes across time points ($F(2, 39) = 4.508$, $p = 0.017$). Again, Bonferroni-adjusted multiple comparison indicated significant drop from T3 to T4 (adjusted $p = 0.014$). All remaining pair-wise comparisons did not show significant mean differences. When we apply standard threshold of 1.5nmol/l for changes in cortisol level from the baseline (Miller et al., 2013), we classified participants into 19 stress responders and 22 non-responders.

3.2. Hierarchical Bayesian computational modeling results

We used computational modeling and hierarchical Bayesian data analysis to disentangle the cognitive processes underlying prosocial behaviors. Eight candidate computational models were compared (see Methods), and the $M6_{pref}$ model yielded the lowest leave-one-out cross-validation information criterion value (Table 1), indicating that the model with social distance based on post-experiment preference ratings (SD_{pref}) outperformed models with pre-defined social distance measures. Moreover, compared to the original hyperbolic social discounting model (M1; Jones and Rachlin, 2006), the exponential models incorporating self-reward sensitivity (M4) and inequality aversion for money-sharing behaviors (M6) provided better fits to the behavioral data. Each motivational factor differentially influenced estimates of other-regarding value (Fig. 2A). Fig. 2B shows the posterior mean parameter estimates as follows: social discounting sensitivity (k: 0.006–0.0138; mean $=$ 0.0477), self-reward sensitivity (β: 0.095–1.76; mean $=$ 0.70), inequality aversion (ρ: 0.02–0.78; mean $=$ 0.17), and inverse temperature (τ: 0.02–2.26; mean $=$ 0.37). Predicted responses generated from the winning model with the estimated parameters were highly correlated with observed responses ($r = 0.95$; $p < 0.001$; Fig. 2C), and the parameter recovery of the winning model indicated reliable estimates across different compositions of the parameters within the estimated parameter range of the participants (**Fig. S3**). Individual-level predicted versus observed responses are shown in **Fig. S4**. Trial-by-trial subjective decision values—including generous decision values (SV_g), other-regarding values (V_{other}), and self-regarding values (V_{self})—were derived from the winning model and subsequently used in model-based general linear model (GLM) analyses.

Table 1

Explanation and comparison results of the computational models.

Model	Model Equation	Parameters	LOOIC	ΔLOOIC
M1	$SV_G = \dfrac{A_o}{1 + kSD} - v_S$	k, τ	4671.5	−1038.2
M2	$SV_G = A_o e^{-kSD} - v_S$	k, τ	6657.8	−3024.5
M3	$SV_G = \dfrac{A_o}{1 + kSD} - \beta v_S$	k, τ, β	4089.9	−456.6
M4	$SV_G = A_o e^{-kSD} - \beta v_S$	k, τ, β	5925.5	−2292.2
M5	$SV_G = \dfrac{A_o}{1 + kSD} - \rho IN - \beta v_S$	k, τ, β, ρ	3947.5	−314.2
M6	$SV_G = A_o e^{-kSD} - \rho IN - \beta v_S$	k, τ, β, ρ	3676.9	−43.6
$M5_{pref}$	$SV_G = \dfrac{A_o}{1 + kSD_{pref}} - \rho IN - \beta v_S$	k, τ, β, ρ	3924.1	−290.8
$M6_{pref}$	$SV_G = A_o e^{-kSD_{pref}} - \rho IN - \beta v_S$	k, τ, β, ρ	3633.3	0

$\boldsymbol{v_S}$ is the net incentive amount for the self, calculated as the trial's incentive amount (the number displayed next to the target information on the screen) subtracted from the amount received for selecting the generous option under a given condition (ranging from −1 to 33). IN represents the degree of self-disadvantage for selecting generous decisions (unequal condition: 20, equal condition: 0). A_o denotes the generous amount allocated to the target (Unequal condition: 30, equal condition: 20). $\boldsymbol{k}$ is the social distance sensitivity. SD represents the social distance information. SD_{pref} refers to the social distance based on preference information. $\boldsymbol{\beta}$ is the self-reward sensitivity. $\boldsymbol{\rho}$ denotes disadvantageous inequality aversion. LOOIC stands for the leave-one-out cross-information criterion. ΔLOOIC indicates the changes in the LOOIC value compared to the winning model.

3.3. Individual differences associated with cortisol levels

The more participants disliked disadvantageous inequality, the fewer generous decisions they made during unequal condition, showing a significant negative correlation between inequality aversion and generous decision ($r(39) = -0.51$; $p < 0.001$; Fig. 3A). However, inequality aversion did not predict generosity decisions under equal conditions ($r(39) = 0.10$, $p = 0.54$; Fig. 3B). Participants with higher levels of inequality aversion showed less generous behavior in the unequal condition, as inequality aversion was positively correlated with the difference in generous decisions between the equal and unequal conditions ($r(39) = 0.57$; $p < 0.001$). Additionally, the log-transformed CORT at T3 was negatively correlated with the inequality aversion ($r(39) = -0.321$; $p = 0.041$; Fig. 5A) and positively correlated with the normalized prosocial decision frequency in the inequality condition ($r(39) = 0.332$; $p = 0.034$), indicating that the higher the cortisol level, the more likely a participant was to make a generous decision in the unequal

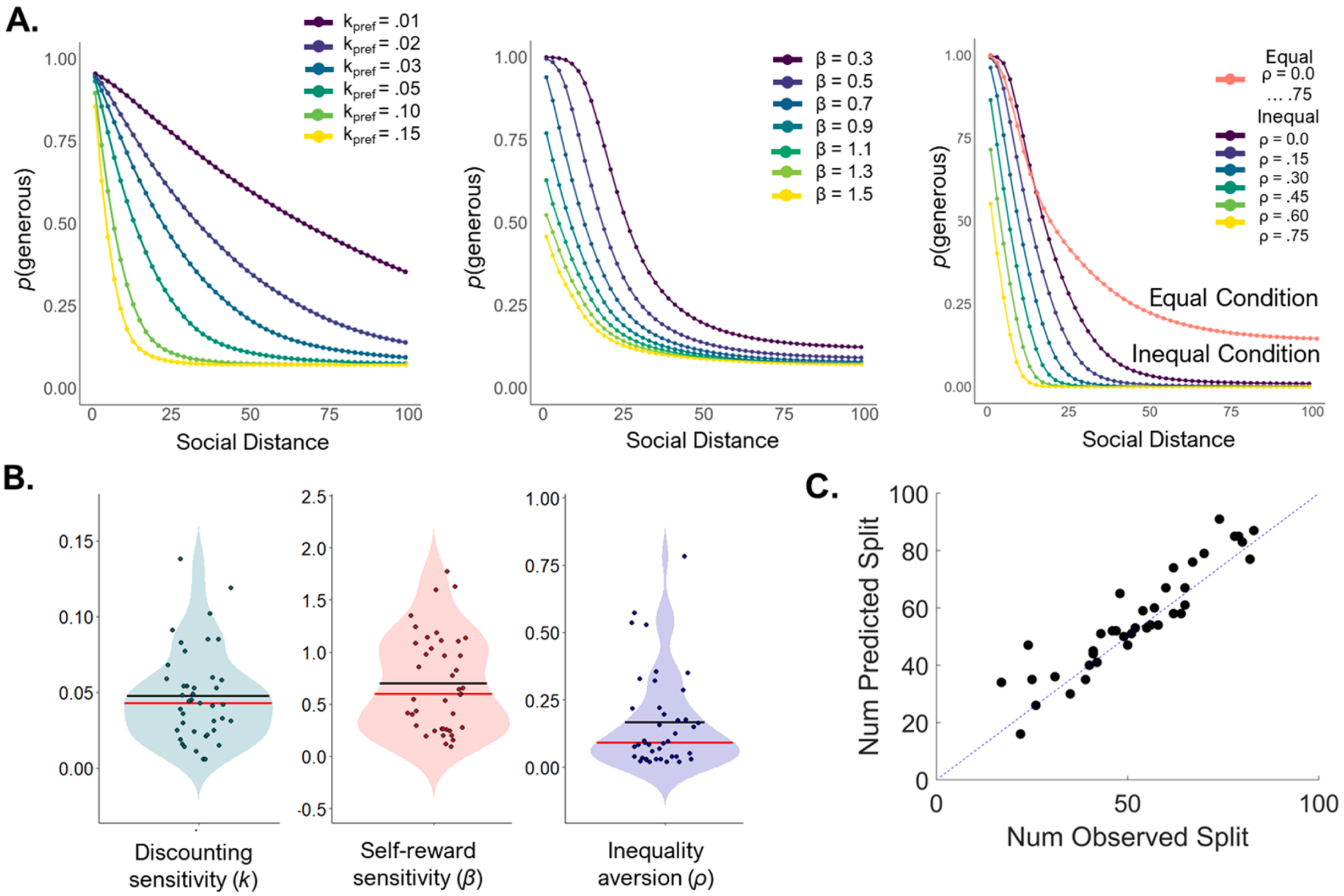

Fig. 2. Model simulation and parameter estimation. (A) Simulation plot illustrates the effect of changes in each parameter on SV_g values. The parameter k is proportional to the probability of making generous decisions, but only with close friends (left panel). The parameter β consistently decreases the probability of sharing as the social distance increases (middle panel). An increase in disadvantageous inequality aversion (ρ) decreases the likelihood of money-sharing in the unequal condition but not affect the equal condition (right panel). (B) Violin plots of estimated parameters: These plots display the estimated ranges of social preference sensitivity, self-reward sensitivity, and disadvantageous inequality aversion. Black lines indicate the mean, and red lines indicate the median of the parameter estimates. (C) Scatter plots demonstrating that the predicted generous decisions, based on the winning model, closely replicate the actual generous decisions made by participants ($r(39) = 0.95$, $p < 0.001$). k: Level of discounting sensitivity, β: Self-reward sensitivity, SV_g: Subjective value for generous decisions.

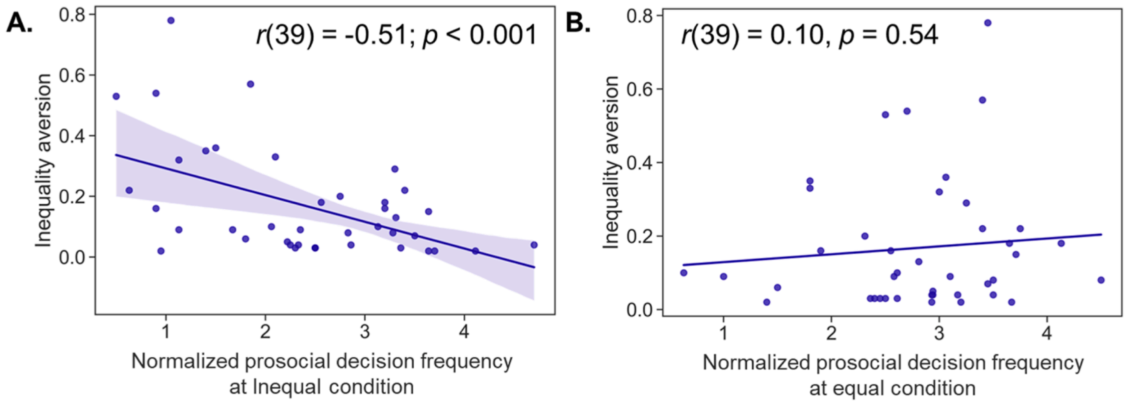

Fig. 3. Scatter plots of money-sharing decision frequencies by condition. A) In the equal condition, there is no significant correlation between individual money-sharing choice frequency and inequality aversion scores. B) In the unequal condition, there is a negative correlation between individual money-sharing choice frequency and inequality aversion scores. To account for individual differences in preferences for generous decisions, the money-sharing choice frequency was normalized at the individual level.

condition. We observed no significant correlation between cortisol and generous behavior at T1, T2, and T4. Trait anxiety (measured via self-report) was not significantly correlated with cortisol levels prior to the experiment ($r(39) = 0.202$, $p = 0.205$) or with disadvantageous inequality aversion ($r(39) = 0.108$, $p = 0.502$). However, it was significantly correlated with baseline cortisol levels ($r(39) = 0.311$, $p = 0.048$).

3.4. Neuroimaging results

3.4.1. Neural correlates of self- and other-regarding value computation

To investigate trial-by-trial neural correlates associated with the subjective value of generous decisions (i.e., SV_g), we conducted a whole-brain parametric modulation analysis during the presentation of the target and incentive. This analysis identified significant activation in the mPFC (MNI: $x = -8$, $y = 56$, $z = -8$, $T = 5.52$, family-wise error corrected at the peak level [FWEp] = 0.02; Fig. 4A **Table S1**) and the precuneus (MNI: $x = 4$, $y = -54$, $z = 28$, $T = 6.26$, FWE$p = 0.003$) as regions reflecting changes in decision value on a trial-by-trial basis. When the parametric modulators were substituted from SV_g to V_{other}, the

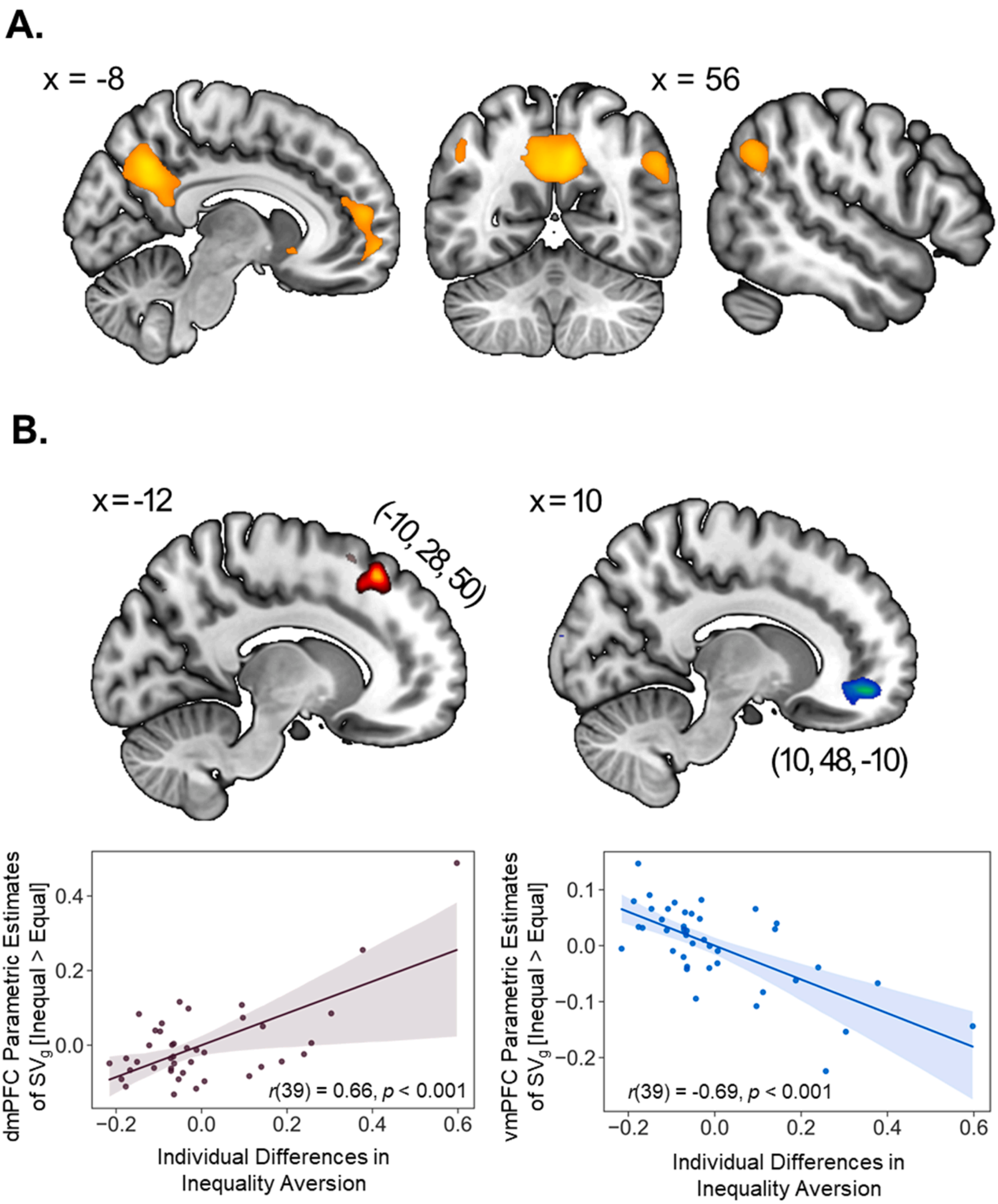

Fig. 4. Neural correlates of other-regarding value processing. (A) Brain regions involved in other-reward processing: Brain regions displaying group-level, trial-by-trial changes in SV_g during the presentation of target information and self-incentive levels include the mPFC, bilateral TPJ, and precuneus. These regions collectively contribute to other-reward processing regardless of the condition (whole-brain peak p value < 0.001; FWE cluster-wise correction, FWE$p < 0.05$). (B) mPFC subregions and inequality aversion: Within mPFC subregions, distinct neural responses are observed concerning the parametric effects of subjective value, which vary according to individual differences in disadvantageous inequality aversion. Individuals with higher inequality aversion show enhanced encoding of the subjective value of generous decisions in the dmPFC, whereas those with lower inequality aversion exhibit correlations in the vmPFC (small volume correction, FWE$p < 0.05$). The values in the correlation plots are residuals derived from partial correlations in a second-level GLM analysis that included inequality aversion as a covariate. SV_g: Subjective value for generous decisions, mPFC: medial prefrontal cortex, dmPFC: dorsal medial prefrontal cortex, vmPFC: ventral medial prefrontal cortex, FWE: family-wise error rate, FWEp: family-wise error at the peak voxel level, GLM: general linear model.

mPFC again showed significant modulation (MNI: $x = 4$, $y = 58$, $z = -8$, FWE$p = 0.025$), along with the bilateral temporal parietal junction (right TPJ, MNI: $x = 54$, $y = -54$, $z = 28$, FWE$p = 0.042$; left TPJ, MNI: $x = -48$, $y = -60$, $z = 36$, FWE$p = 0.047$), and the precuneus (MNI: $x = 6$, $y = -58$, $z = 34$; Fig. 3A). No significant brain regions were identified when V_{self} was used as the parametric modulator.

3.4.2. *Individual differences in computing the value of generous decision*

Based on the behavioral results, we hypothesized that individuals who are averse to disadvantageous inequality would differentially compute SV_g between the unequal and the equal condition when making a generous decision. Our findings confirmed this expectation.

The beta estimates of SV_g were positively correlated with inequality aversion in the dmPFC (MNI: $x = -10$, $y = 28$, $z = 50$, FWE$p = 0.021$, small-volume-corrected (SVC); Fig. 4B Left) and negatively correlated in the vmPFC (MNI: $x = 10$, $y = 46$, $z = -6$, FWE$p = 0.01$, SVC; Fig. 4B Right, **Table S2**). These results suggest that participants with higher levels of inequality aversion encoded SV_g more positively in the dmPFC and more negatively in the vmPFC during the unequal vs. equal condition.

The parameter SD_{pref} is the primary external information that is needed to calculate SV_g and varies on a trial-by-trial basis. Considering this, we next conducted a parallel analysis using SD_{pref} and $Amount_{self}$ to investigate individual differences in the neural processing of self- and other-related information for generous decisions. Results demonstrated that neural regions encoding SD_{pref} as a function of inequality aversion overlapped with those encoding SV_g (**Fig. S5A**) positively in the dmPFC (MNI: $x = -10$, $y = 28$, $z = 50$, $T = 5.6$, FWE$p = 0.003$, SVC; **Fig. S5B left**) and negatively in two regions of the vmPFC (MNI: $x = 10$, $y = 50$, $z = -8$, $T = 5.96$, FWE$p = 0.001$, SVC; MNI: $x = 10$, $y = 48$, $z = -24$, $T = 4.98$, FWE$p = 0.017$, SVC; **Fig. S5B right**). An exploratory whole-brain analysis of the SD_{pref} parametric modulation map revealed additional regions of the bilateral TPJ (MNI: $x = 36$, $y = -64$, $z = 40$, $T = 5.09$, FWEc < 0.001; MNI: $x = -42$, $y = -46$, $z = 48$, $T = 3.91$, FWEc $= 0.041$, **Table S3**).

No brain regions were significantly associated with $Amount_{self}$ as a function of inequality aversion within our a priori mPFC mask, but the whole-brain exploratory analysis revealed that the fusiform gyrus (MNI: $x = 40$, $y = -12$, $z = -38$, $T = 5.71$, FWEc $= 0.008$), the left middle occipital lobe extending into the left TPJ (MNI: $x = -30$, $y = -66$, $z = 36$, $T = 5.5$, FWEc < 0.001; **Fig. S7**), and the right middle temporal lobe extending into the right TPJ (MNI: $x = 50$, $y = -74$, $z = 24$, $T = 5.34$, FWEc < 0.001, **Fig. S7, Table S4**) were positively correlated with the self-reward amount during the equal vs. unequal condition as a function of inequality aversion.

Individuals with higher levels of inequality aversion showed reduced generosity in the unequal condition, possibly due to greater sensitivity to self-regarding rewards when making selfish decisions. Supporting this hypothesis, a whole-brain analysis revealed that participants with higher levels of inequality aversion exhibited significant encoding of trial-by-trial changes in V_{self} in specific brain regions, such as the orbitofrontal cortex (MNI: $x = 18$, $y = 52$, $z = -16$, $T = 5.95$, FWE$p = 0.014$) and the hippocampus (MNI: $x = 36$, $y = -16$, $z = -12$, $T = 5.79$, FWE$p = 0.021$; **Table S5**).

3.4.3. *Mediation analysis results: neural processes mediating the link between cortisol levels and inequality aversion*

We also investigated the neural correlates of cortisol concentration and inequality aversion by examining how cortisol levels affect the processing of self-regarding ($Amount_{self}$) and other-regarding rewards (V_{other}), and SD_{pref}, in the contrast map of the unequal vs. equal condition. This was done while controlling for inequality aversion and cortisol reactivity. A significant negative correlation was found between cortisol levels and the encoding of $Amount_{self}$ in the left dmPFC (MNI: $x = -16$, $y = 34$, $z = 62$, $p < 0.001$, uncorrected, **Fig. S6**), indicating that higher cortisol levels diminish the encoding of self-regarding rewards under the unequal condition. No significant correlations were observed between cortisol levels and brain regions encoding SD_{pref} or SV_g.

Additionally, we investigated whether cortisol levels are associated with neural regions encoding SV_g and SD_{pref}—specifically those regions that are negatively correlated with inequality aversion. Individual vmPFC beta estimates of SD_{pref} (peak voxel MNI: $x = 10$, $y = 50$, $z = -8$) and cortisol concentration levels were positively correlated ($r(39) = 0.42$, $p < 0.01$), whereas SV_g-related activity was not significantly correlated. To test how individual differences in the processing of SD_{pref} and $Amount_{self}$ influence the degree of disadvantageous inequality aversion, two mediation analyses were conducted independently. For SD_{pref}, individual parameter estimates of the vmPFC (peak voxel MNI: $x = 10$, $y = 50$, $z = -8$) was assigned as a mediator. For $Amount_{self}$, the dmPFC (peak voxel MNI: $x = -9$, $y = 30$, $z = 48$) parameter estimates extracted from the conjunction (Fig. S6) was assigned as a mediator to explore the relationship between cortisol concentration and disadvantageous inequality aversion. The mediation analysis revealed that dmPFC encoding of $Amount_{self}$ partially mediated the relationship between lower cortisol levels and increased inequality aversion (partial indirect effect: $B = 0.007$; standard error [SE] $= 0.002$; 95 % CI: 0.0001–0.0077; Fig. 5C). Another mediation analysis demonstrated that strong vmPFC encoding of SD_{pref} mediated the relationship between higher cortisol levels and decreased disadvantageous inequality aversion (indirect effect: $B = -0.0045$, SE $= 0.0025$, 95 %CI: -0.0104 to -0.006; Fig. 5D), suggesting that vmPFC activity tracking SD_{pref} is a key neural mechanism underlying cortisol-related increases in money-sharing behaviors.

3.4.4. *Effective connectivity analysis results*

We conducted an exploratory effective connectivity analysis to investigate the influence of cortisol on the connectivity between the neural regions involved in value computation during generous behaviors. For this purpose, we employed dynamic causal modeling (DCM), a tool widely used to infer causal relationships among distributed neural regions in fMRI data. Additionally, we utilized parametric empirical Bayes (PEB) analysis to identify the most credible group-level model, based on the estimated DCMs to investigate both group-level patterns and individual differences in effective connectivity. Our approach involved implementing a DCM-PEB analysis to assess the modulatory effects of cortisol on generous compared to selfish decisions (see Supplementary Information for details). The Bayesian contrast between generous and selfish decisions for each connectivity type revealed interesting results. Specifically, cortisol exhibited positive modulatory effects on connectivity from the VS to the dmPFC and from the VS to the DS. In contrast, we observed negative modulatory effects from the DS to the VS and from the DS to the dmPFC ($p < 0.05$, two-tailed; Fig. 5B, **Table S6**).

4. Discussion

This study aimed to clarify the effects of social stress on prosocial decisions, addressing ambiguities found in prior research. Under stress, individuals tend to rely more on intuitive rather than deliberative decision-making, which may explain the increased generosity observed under disadvantageously unequal conditions. Our findings suggest that participants with higher cortisol levels showed less sensitivity to the inequality of the situation, leading to prosocial behavior similar to that in the equal conditions. Neuroimaging data revealed that stress was associated with increased activity in the vmPFC (linked to intuitive decisions) and decreased activity in the dmPFC (linked to deliberative thinking). Additionally, effective connectivity analysis showed that stress interfered with processing disadvantageous inequality by altering the corticostriatal loop. These results indicate that stress reduces the cognitive effort required to process disadvantageous inequality, promoting more generous behavior in these contexts.

We utilized a modified social discounting task that incorporated

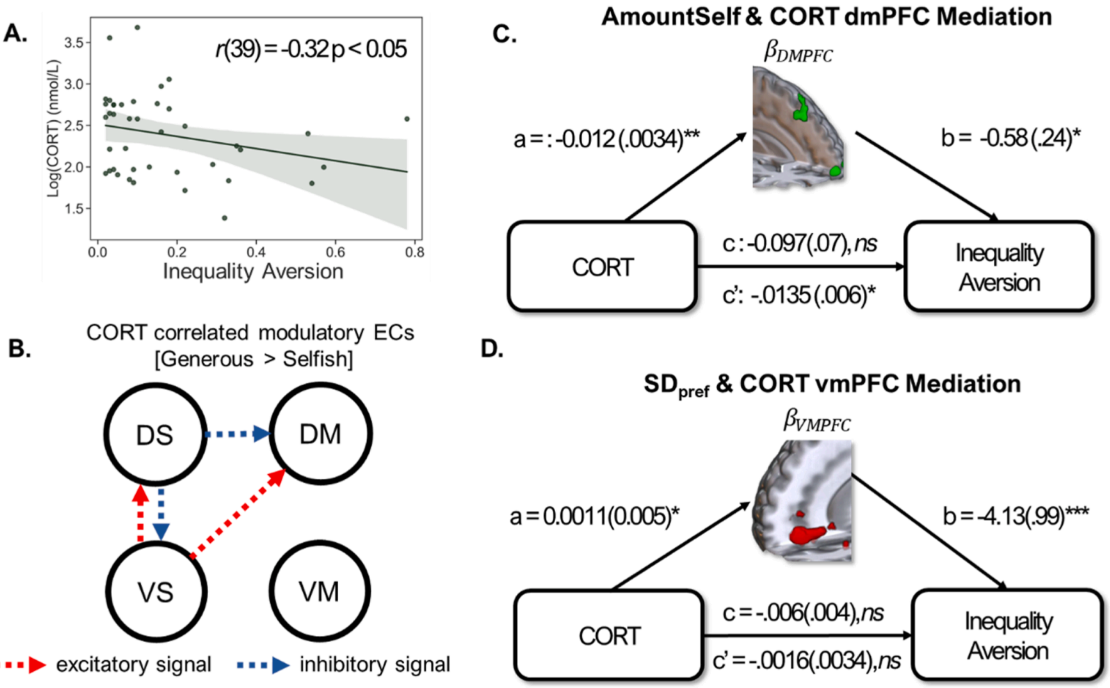

Fig. 5. Mediation analysis and effective connectivity between cortisol and inequality aversion. (A) Correlation between cortisol and inequality aversion: The log-transformed cortisol level at T3 was negatively correlated with the inequality aversion parameters. (B) Effective connectivity analysis: Schematic representation of the effective connectivity analysis for generous versus selfish decisions, illustrating the influence of cortisol on modulatory effective connectivity. Positive effects were observed in the connections from the VS to the dmPFC and from the VS to the DS, while negative effects were found in the connections from the DS to the VS and from the DS to the dmPFC. Blue dotted lines indicate decreased modulatory strength, while red dotted lines indicate increased modulatory strength. (C) Mediation model with dmPFC: A mediation model was constructed with CORT as the independent variable, inequality aversion as the dependent variable, and the dmPFC parameter estimate (correlated with $\text{Amount}_{\text{self}}$ as a function of CORT) as the mediating variable. The analysis showed a partial mediation effect of CORT on inequality aversion through dmPFC estimates. (D) Mediation model with vmPFC: An alternative mediation model, similar to the one (C), was constructed but replaced dmPFC with beta estimates of the vmPFC. The vmPFC activities were parametrically modulated by SD_{pref} as a function of inequality aversion. The vmPFC beta estimates fully mediated the effect of CORT on inequality aversion. CORT: cortisol level, dmPFC (DM): dorsal medial prefrontal cortex, DS: dorsal striatum, EC: effective connectivity, mPFC: medial prefrontal cortex; SD: social distance, vmPFC (VM): ventral medial prefrontal cortex, VS: ventral striatum.

disadvantageous and unequal options to examine the effects of stress across a broader range of behavioral responses. To disentangle the motivational components underlying these decisions, we employed computational modeling combined with hierarchical Bayesian data analysis. This approach helped us differentiate between social discounting preference sensitivity, self-reward sensitivity, and aversion to disadvantageous inequality. Our proposed model outperformed traditional social discounting models in predictive accuracy. Behaviorally, cortisol levels were inversely related to inequality aversion but not to social preference sensitivity, replicating prior findings that stress enhances prosocial sharing in males. Neurally, individual differences in inequality aversion were linked to the degree to which the dmPFC encoded changes of SVg and SD_{pref}, while vmPFC activity negatively correlated with both parametric modulators. Mediation analyses revealed that the decrease in inequality aversion due to elevated cortisol levels was indirectly mediated by these distinct MPFC subregions. Overall, our findings suggest that distinct patterns of prosocial behavior may emerge depending on two key factors: (1) the association between specific components of behavioral tasks (e.g., calculating monetary or social gains and losses for oneself or others) and distinct neural circuits, including mPFC subregions (e.g., vmPFC vs. dmPFC), and (2) the specific neural circuits activated by stress within a given individual.

4.1. *Social stress promotes intuitive prosocial decisions*

In this study, we explored how individual differences in inequality aversion influence prosocial decision-making. Participants with higher inequality aversion tended to consider contextual information and maximize self-interest under disadvantageous unequal conditions, while those with lower inequality aversion were less influenced by their own relative disadvantage when making prosocial decisions. Prior research has shown that economic decision tasks typically elicit intuitive money-sharing behaviors, whereas reflective, strategic participants often act in self-serving ways (Rand et al., 2012; Lotz, 2015; Yamagishi et al., 2016). Our findings suggest that stress makes individuals more generous under disadvantageously unequal conditions, supporting earlier findings (Margittai et al., 2015; Margittai et al., 2018). This increase in prosocial behavior under stress may stem from a shift toward more intuitive, less deliberative processes, as stress has been shown to reduce reflective processes and promote reflexive, habitual responses (Yu, 2016; Lenow et al., 2017; Zerbes et al., 2022). Recent meta-analyses further suggest that stress tends to promote prosocial behaviors in less complex decision scenarios (Nitschke et al., 2022), with limited modulation by factors such as stressor type, gender, delay duration, and the number of decisions.

There are alternative explanations for stress-induced changes in prosocial decision-making. For example, stress could influence sensitivity to personal loss or alter risk preferences (Porcelli and Delgado, 2009). However, our analyses did not provide evidence supporting these factors as primary drivers in our study. Specifically, we found no significant correlations between cortisol levels and model parameters related to self-reward sensitivity or social discounting sensitivity, which would indicate changes in how participants value personal rewards versus social considerations. Additionally, our test of the exponential alpha parameter from prospect theory, which reflects diminishing sensitivity to monetary payoffs, did not converge, further suggesting that stress did not modulate risk sensitivity. Instead, our findings consistently pointed to social distance, self-reward sensitivity, and disadvantageous inequality aversion as the key motivators behind the observed prosocial behavior under stress. While alternative explanations are plausible, our data strongly supports inequality aversion as a central factor influencing stress-induced changes in prosocial decisions.

4.2. Neural underpinnings of generosity in social discounting tasks

We found that individuals with lower inequality aversion showed parametric tracking of changes in SV_g and SD_{pref} in the vmPFC, a key neural hub for intuitive prosocial decision-making (Zaki and Mitchell, 2013; Kim, 2020). This region is activated when resolving social inequalities (Tricomi et al., 2010) and is notably active during generous decisions in social discounting tasks (Strombach et al., 2015). Mediation analyses indicated that cortisol increased sensitivity to SD_{pref} in the vmPFC, which in turn indirectly mediated the decrease in inequality aversion. Stress facilitates habitual behaviors by enhancing vmPFC and VS activities (Yu, 2016; Ironside et al., 2018), binding to glucocorticoid receptors in the limbic system and vmPFC, and increasing excitatory neurotransmission in these areas (Popoli et al., 2012; Pizzagalli, 2014; Mcklveen et al., 2015). Stress also affects the mesolimbic dopaminergic pathway (Douma and de Kloet, 2020), critical for oxytocin-dependent social interactions in rodents (Hung et al., 2017). Importantly, dopaminergic processing of social rewards appears to be critical for signaling prosocial motivations, as blocking dopamine receptors has been shown to eliminate sex-specific generosityin similar paradigms (Soutschek et al., 2017). Together, these findings provide novel insights into how stress modulates intrinsic social reward processing, although further research is needed to elucidate the precise neural mechanisms by which stress influences prosocial value computations.

4.3. Neural regions associated with deliberative decisions and stress effects

Our study showed that individuals making fewer prosocial decisions under disadvantageous conditions exhibited dmPFC activity that parametrically encoded other-regarding values and social distance based on preference information. The dmPFC integrates external information crucial for deliberative decisions (Kim, 2020). In the delay discounting task, it encodes future rewards and time delays (Wang et al., 2021). In addition, dmPFC activity reflects the degree of self-other merging in competitive or cooperative tasks (Wittmann et al., 2016), and modulation of the dmPFC can affect the calibration of responses that integrate self and others' capabilities (Wittmann et al., 2021). Interestingly, this region is more robustly activated among selfish individuals when making prosocial decisions (Sul et al., 2015), suggesting a greater cognitive demand in such contexts. Furthermore, the dmPFC is crucial for flexible switching behaviors for optimal action selection (Domenech et al., 2020). Combining these theoretical and empirical studies, we suggest that the dmPFC is involved in computing other-regarding values by analyzing information from the external environment when it is necessary to carefully weigh the balance of benefits between oneself and others. We also observed that heightened sensitivity to self-reward in the disadvantageous unequal condition was negatively correlated with post-stress cortisol levels, suggesting that stress impairs the processing of external information needed for optimal self-benefiting decisions. This interpretation aligns with evidence indicating that stress impairs cognitive flexibility (Schwabe and Wolf, 2011). Stress can also cause a whole-brain reconfiguration of neural networks, upregulating salience networks while downregulating cognitive systems (Hermans et al., 2014; Zhang et al., 2020; Wang et al., 2022), as well as imparing working memory (Roozendaal et al., 2009) and goal-directed control (Vinkers et al., 2013). These changes may result in a tendency to rely on established policies and routines, as observed in studies of stress-induced overreliance on habits (Lenow et al., 2017; Cremer et al., 2021).

Importantly, rodent studies have provided valuable insights into the neural circuitry underlying stress-induced changes in decision-making processes. For example, the bidirectional dmPFC-mediodorsal thalamus (MD) pathway is critical for updating reward values following outcome devaluation. Disruption of the thalamus-to-cortex direction of this pathway hinders the updating of action-reward contingencies (Alcaraz et al., 2018). The connection between the dmPFC and DS is also essential for sustaining goal-directed behaviors (Hart and Balleine, 2016). Notably, modulation of dmPFC projections to the MD (i.e., dorsal loop) leads to delayed responses in sequential response tasks, whereas modulating vmPFC projections to the MD (i.e., ventral loop) leads to premature choices (De Kloet et al., 2021). Furthermore, acute stress rapidly increases functional connectivity between the amygdala and DS, promoting a shift toward habitual responses and blocking mineralocorticoid receptors—another type of cortisol receptors—not only prevents a shift toward habitual responding but also attenuates stress-induced increases in striatal-amygdala connectivity (Vogel et al., 2017). Consistent with previous literature, we observed opposite influences of CORT on corticostriatal effective connectivity to the dmPFC during generous decisions, which may reflect a stress-induced disruption of the dorsal loop that is crucial for maintaining deliberative cognitive processing. Our effective connectivity analyses further elucidated differential effects of CORT across mPFC subregions: disruption of the dorsal loop may have hindered the transmission of decision values for generous decisions from the dmPFC to the vmPFC (Domenech et al., 2020). Together, these findings support a functional dissociation between the ventral and dorsal cortico-thalamic loops under stress, demonstrating that stress fosters intuitive prosocial decisions while interfering with utility-maximizing strategic value computation by differentially modulating activity in the ventral and dorsal subregions of the mPFC.

4.4. Limitations and future direction for prosocial-related stress research

Our study has several limitations that warrant consideration. First, the effectiveness of our stress induction procedure requires further validation. Although we categorized participants based on a standard threshold, individual differences in stress reactivity remain a challenge in stress research. While our stressor was designed to enhance internal validity by focusing solely on social stress within the scanner, this approach may have limited its overall effectiveness compared to multicomponent stress tasks like the Maastricht Acute Stress Test (MAST). While stronger stressors such as MAST can elicit more robust physiological responses, their implementation would have introduced practical complications, including participant fatigue and potential confounds arising from participants exiting and re-entering the scanner. Future studies should explore ways to balance ecological validity and experimental control when selecting stressor tasks Second, the present study included only male participants, based on prior findings that hormonal stress responses in females could vary across menstrual cycle phases (Kirschbaum et al., 1999). While this approach helped to reduce hormonal variability, it limits the generalizability of our findings. Future study should include female participants to determine whether the observed effects extend across sexes or reveal sex-specific differences in the neural mechanisms underlying stress-modulated prosocial decision-making.

Third, while our study provides valuable insights into the neural mechanisms underlying prosocial decision-making under stress, we acknowledge that our task design does not allow for a clear distinction between intuitive and deliberative decision-making processes. Although reaction time data were analyzed as an indirect measure, additional experimental validation—such as cognitive load manipulation or explicit time constraints—would be necessary to more precisely differentiate between these processes. Future research should address this limitation by incorporating tasks that explicitly manipulate cognitive load or impose time constraints to better understand how stress influences intuitive versus deliberative prosociality. Such approaches would provide a more comprehensive framework for interpreting the effects of stress on social decision-making.

Fourth, although our study provides both behavioral and neural evidence supporting stress-related enhancement of prosocial decisions, we cannot rule out the possibility that participants' responses were automatic, reflecting diminished self-regulatory control under stress. The task design itself could have influenced responses by affecting the relative difficulty of selfish versus prosocial choices. Additionally, individuals who are predisposed toward prosocial behavior may continue to express these tendencies under stress. Therefore, future research should explicitly manipulate both individual differences in prosociality and contextual norms surrounding prosocial behavior to determine whether stress genuinely promotes prosociality or merely amplifies existing behavioral predispositions.

Fifth, as our study utilizes a laboratory-based stress induction paradigm, it may not fully capture the complexities of stress dynamics encountered in real-world situations. Future research should incorporate more ecologically valid stress paradigms to assess whether our findings generalize beyond laboratory conditions. For example, longitudinal studies examining workplace stress or social rejection, as well as experience-sampling methods investigating post-stress behaviors in everyday settings, could provide deeper insight into how stress influences human behavior in naturalistic environments.

Sixth, the DCM-PEB analysis has limitations in establishing causal relationships due to its model-dependent assumptions. The DCM-PEB analysis can provide causal relationships among the ROIs for a given model; however, it cannot explain other neural connections contributing to networks outside the model or compare models with different ROIs. Our study is one of the first preliminary studies to provide neural evidence in corticostriatal connections associated with cortisol and these findings need further validation. Future research should provide strong theoretical and empirical evidence selecting ROIs and designing model for DCM-PEB for comparable findings. While alternative methods like Granger causality or TMS/tDCS were suggested, fMRI's temporal resolution constraints hindered their application. To address this, future studies should combine multimodal approaches (e.g., TMS/tDCS) with task-based fMRI to validate causal mechanisms.

Last, while our study employs a hierarchical Bayesian modeling approach to infer decision-making parameters, we acknowledge that our justification for selecting the M6pref model relies primarily on LOOIC comparisons. Future research could strengthen the robustness of our findings by conducting sensitivity analyses using alternative modeling approaches, though the suitability of reinforcement learning or drift-diffusion models for this specific task remains debatable.

5. Summary and conclusion

In summary, we hypothesized that stress hinders strategic behavior in disadvantageous settings by reducing the integration of external information, thereby making self-serving actions more challenging. To test this hypothesis, we employed a modified social discounting task and a computational model to measure each participant's aversion to disadvantageous inequality. Our neural investigation of prosocial value computation under unequal and equal conditions showed that activity in the dmPFC and vmPFC were positively and negatively correlated, respectively, with participants' inequality aversion parameters. Mediation analysis supported our neural findings, showing that increased cortisol concentration mediated a decrease in inequality aversion by increasing neural activity associated with social distance based on preference information while reducing updates of self-regarding rewards. These findings provide new insights into stress-related prosocial decisions, suggesting that stress can promote intuitive prosocial decisions, especially in disadvantageous situations where self-serving actions demand more deliberate processes.

Data/code availability statement

The MATLAB codes for GLM analyses and R and Stan codes for Bayesian computational modeling is available at github: https://github.com/gunil0817/stressSD. The contrast files of the GLMs and behavior data is available at open repository: https://github.com/gunil0817/stressSD.

CRediT authorship contribution statement

Kun Il Kim: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Jeung-Hyun Lee:** Writing – review & editing, Formal analysis, Conceptualization. **Woo-Young Ahn:** Writing – review & editing, Validation, Methodology, Formal analysis. **Hackjin Kim:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121273.

Data availability

Data will be made available on request.

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