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Greed personality trait links to negative psychopathology and underlying neural substrates

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Abstract

Greed personality trait (GPT), characterized by the desire to acquire more and the dissatisfaction of never having enough, has been hypothesized to link with negative emotion/affect characteristics and aggressive behaviors. To describe its emotion-related features, we utilized a series of scales to measure corresponding emotion/affect and aggression ($n = 411$) and collected their neuroimaging data ($n = 330$) to explore underlying morphological substrates. Correlational analyses revealed that greedy individuals show more negative symptoms (e.g. depression, loss of interest, negative affect), lower psychological well-being and more aggression. Mediation analyses further demonstrated that negative symptoms and psychological well-being mediated greedy individuals' aggression. Moreover, exploratory factor analysis extracted factor scores across three factors (negative psychopathology, happiness, and motivation) from the measures scales. Negative psychopathology and happiness remained robust mediators. Importantly, these findings were replicated in an independent sample ($n = 68$). Voxel-based morphometry analysis also revealed that gray matter volumes (GMVs) in the prefrontal-parietal-occipital system were associated with negative psychopathology and happiness, and GMVs in the frontal pole and middle frontal cortex mediated the relationships between GPT and aggressions. These findings provide novel insights into the negative characteristics of dispositional greed, and suggest their mediating roles on greedy individuals' aggression and underlying neuroanatomical substrates.

Key words: greed personality trait; happiness; negative psychopathology; aggression; voxel-based morphometry

Introduction

Greed personality trait (GPT) is often characterized by the experience of desiring more and the dissatisfaction of not having enough. Greed is not only associated with immorality and unethical behavior in philosophy and religion (Seuntjens *et al.*, 2015a, 2019), but has also been considered to be a cause of many financial problems and scandals (Seuntjens *et al.*, 2016, 2019). In particular, greed has been broadly believed to correlate positively with maximization tendencies (Seuntjens *et al.*, 2015a), materialism (Krekels and Pandelaere, 2015), egoism (Krekels and Pandelaere, 2015) and selfishness (Lambie and Haugen, 2019). However, greed is not inherently negative. Economists have highlighted greed's destructive role in financial crises (e.g. subprime mortgage crisis in the United States and debt crisis in Europe) (Mussel *et al.*, 2015) but have also acknowledged its influence in motivating innovation and spurring economic growth (Williams, 2000; Fehr and Gintis, 2007), implying the duality of greed. Nevertheless, much of greed research has been at the behavioral level and its associated cognitive and neural mechanisms remain understudied. Understanding these mechanisms may be informative to how economical habits and moral behaviors are shaped.

Greed has been proposed to have stable negative consequences, especially for adverse emotion/affect experiences. The well-known 'Tragedy of the Commons' is one classic example of the negative consequence of greed on public resource allocation (Hardin, 1968). Considerable empirical evidence has also demonstrated that greedy individuals subjectively experience a series of negative emotions, including unhappiness

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(Seuntjens *et al.*, 2015a), envy (Krekels and Pandelaere, 2015), negative affect after losing money (Mussel and Hewig, 2016), life dissatisfaction (Pavot and Diener, 2009; Seuntjens *et al.*, 2015b) and anger (Vrabel *et al.*, 2019). Indirect evidence suggest that greed is positively associated with several personality traits, such as antagonism, disinhibition, detachment, negative affectivity and psychoticism (Seuntjens *et al.*, 2019; Vrabel *et al.*, 2019). Although the extant literature in the field has focused on the negative outcomes and behaviors of greed, only a few studies have directly explored the negative psychopathological core features of greed, particularly pertaining to symptoms of depression, anxiety and their mixed symptoms, which possibly limits the understanding of the nature of greed and its impacts on mental health. Thus, the present study was aimed to comprehensively delineate dispositional GPT via utilizing field-standard measures of psychopathology to improve our insights of greed.

Our first inquiry of greed's negative association with subjective well-being begins with the investigation of the stable negative consequences of greed behaviors and its definition. Greedy individuals have been proposed to be dissatisfied with their current state of affairs, which in turn, deteriorates their self-esteem and life satisfaction (Seuntjens *et al.*, 2015b). As well-being is multifaceted, consisting of social, psychological and subjective factors, it reflects distinct aspects of one's happiness.

Greedy individuals often resort to aggressive measures to achieve their personal goals and desires (Winarick, 2010). Although the direct empirical evidence to support such view remains scarce, considerable indirect evidence hint at the potential relations between these two constructs. Negative emotional state typically precedes peripheral antagonistic states, such as anger, hostility and nervousness (Donahue *et al.*, 2014; Kovácsová *et al.*, 2016), that culminate into physical aggression (Garofalo and Velotti, 2017). Further, emotion dysregulation is believed to play a critical mediating role in the associations between negative emotion/affect and aggression (Velotti *et al.*, 2019; Puhalla and McCloskey, 2020). Thus, we sought to directly examine whether greed is positively associated with aggressive tendencies.

Although studies on greed using survey methods are increasingly growing, supplemental investigations on the neural substrates underlying the greed are relatively rare. Evidence from electroencephalography (EEG) and magnetic resonance imaging (MRI) studies have predominantly been concerned with how greedy individuals' decision making and their underlying neural substrates. EEG studies on greed reported reduced feedback-related negativity difference between unfavorable and favorable outcomes (Mussel *et al.*, 2015), and decreased P300 effect to positive feedback in greedy individuals (Mussel and Hewig, 2019), suggesting altered learning capacity from prior experiences and feedback. One functional MRI study also observed a neural mediating mechanism underlying the associations between GPT and behavioral loss aversion via activations in the ventromedial prefrontal cortex (VMPFC) and medial orbitofrontal cortex (Li *et al.*, 2019). Further, two recent fMRI studies directly examined the neuroanatomical and functional substrates of GPT combining univariate and multivariate pattern analysis approaches (Wang *et al.*, 2021a, 2021c). At the morphological level, grey matter volumes (GMVs) on the lateral frontal pole cortex (FPC), VMPFC and lateral occipital cortex (LOC) were found to significantly predict individual variability on greed (Wang *et al.*, 2021a). At the functional level, reward-related brain activations on the lateral OFC and prospection network system, including the dorsolateral PFC (DLPFC), dorsomedial PFC (DMPFC), superior parietal lobule (SPL) and anterior cingulate cortex (ACC) were associated with GPT scores (Wang *et al.*, 2021a). Additionally, reward-related static and dynamic functional networks have been demonstrated to be important in supporting greed(Wang *et al.*, 2021a). Taken together, the morphological and functional characteristics of the prefrontal cortex are associated with greed. Considering the possible link between GPT and aggression, we thus further explored the neural substrates underlying the associations between greed and aggression, and hypothesized that the prefrontal cortex subsurving into reward and prospective thinking may be a potential candidate region for understanding the effects of greed on social behaviors.

In the current study, we collected data utilizing a large number of questionnaires related to negative emotions, happiness, and social behavior, in addition to individual structural imaging data in a relatively large sample ($n = 411$), aiming to comprehensively depict the characteristics of dispostional greed and its associations to negative psychopathology and maladaptive social behaviors (i.e. aggression). Furthermore, we explored whether these negative psychopathological characteristics mediated the associations between greed and aggression. We then employed exploratory factor analyses (EFAs) to extract the common latent factors relevant to greed. Finally, we investigated the neuroanatomical substrates underlying these main factors and mediation effects on the GMV from a explorative perspective.

Materials and methods

Participants

A total of 497 college students participated in this study. Eighteen participants were removed from final analysis due to incomplete ($n = 12$) and low quality data ($n = 6$) for a final sample of 479 (64.5% females, age ranged from 17 to 28 years old). Participants were further divided into two datasets. The first included 411 participants (65.9% females, age $M \pm SD = 19.93 \pm 1.47$), whose results were reported in the main text. The second dataset included 68 participants (55.9% females, age $M \pm SD = 20.72 \pm 1.74$) which provided replication validation analysis. In the first dataset, 330 participants simultaneously had T1-weighted imaging data (sub-dataset 1). No participant self-reported any history of neurological or psychiatric issues. Written informed consent was obtained from all adult participants (age 18–28) before formal investigation. Five adolescent participants (age 17) were required to sign the consent form after receiving the verbal consent from their parents. This study was approved by the Institutional Review Boards of Tianjin Normal University (No. XL2020-27), China.

Measures and questionnaires

Greed personality trait

GPT was measured by the 7-item Dispositional Greed Scale (Seuntjens *et al.*, 2015b; Mussel *et al.*, 2018) where participants rated their degree of agreement with each statement describing greedy tendencies, $\alpha = 0.749$.

Depression and anxiety

Depression was measured using the Beck Depression Inventory (BDI) using a 4-point continuum of statements representing the degree of severity of depression symptomology, $\alpha = 0.902$. Capturing the tripartite model of both anxiety and depression was the Mood and Anxiety Symptoms Questionnaire (MASQ) (Clark and Watson, 1991), $\alpha = 0.922$. The MASQ captures three aspects of general distress: (i) mixed symptoms (15 items), (ii) depressive symptoms (12 items) and (iii) anxious symptoms (11 items). Further, the MASQ also measures two additional sets of symptomologies: (iv) anxious arousal (17 items) and (v) anhedonic depression (22 items). Lastly, the Beck Anxiety Inventory (BAI) (Beck *et al.*, 1961) was used to measure severity of an individual's experience of anxiety, $\alpha = 0.902$.

Affect

The Positive and Negative Affect Schedule (PANAS) was used to measure experience of positive and negative affect (Watson *et al.*, 1988). Participants rated the degree to which they experienced different feelings and emotions across (i) Positive (10 items, e.g. 'excited') and (ii) Negative affect experiences (e.g. 'distressed') within the past week.

Aggression

Aggression was measured using the Buss-Warren Aggression Questionnaire (BWAQ) (Buss and Warren, 2000) and the Reactive-Proactive Aggression Questionnaire (RPQ) (Raine *et al.*, 2006). The BWAQ is a 34-item instrument that measures five dimensions of trait aggression: (i) physical aggression, (ii) verbal aggression, (iii) anger, (iv) hostility and (v) indirect aggression, $\alpha = 0.890$. The RPQ is a 23-item instrument that measures trait tendencies to engage in (i) proactive aggression ($\alpha = 0.839$, i.e. instigating aggression and antagonizing others) and (ii) reactive aggression ($\alpha = 0.825$, i.e. impulsive responses to threat and provocation).

Well-being

Psychological well-being was measured with the 84-item Psychological Well-Being Scale (PWBS) (Ryff and Keyes, 1995) consisting of six distinct dimensions: (i) autonomy, (ii) environmental mastery, (iii) personal growth, (iv) positive relations, (v) purpose in life and (vi) self-acceptance, $\alpha = 0.801$. Social well-being was measured using the 15-item Social Well-Being Scale (SWBS) (Keyes, 1998) consisting of five dimensions: (i) social integration, (ii) social contribution, (iii) social coherence, (iv) social actualization and (v) social acceptance, $\alpha = 0.864$. Lastly, we captured subjective happiness using the Subjective Happiness Scale (SHS) (Lyubomirsky and Lepper, 1999). The SHS assesses an individual's broad, global subjective happiness using both self-report and self-comparison items.

Work preference

Work preference was measured using the 30-item Work Preference Inventory (WPI) (Amabile *et al.*, 1994) across two broad motivational orientations: (i) Intrinsic Motivation and (ii) Extrinsic Motivation. Intrinsic motivation comprised of two additional subdimensions capturing personal challenge and enjoyment while the Extrinsic motivation comprised of preferences for outward recognition and compensation, $\alpha = 0.810$.

Brain imaging data acquisition

Whole-brain imaging data were collected using a Siemens 3 T Prisma scanner with a 64-channel head coil at the Center for MRI Research of Tianjin Normal University. Participants laid supine on the scanner bed with foam pads reduce and minimize head motion. High-resolution T1-weighted structural images were extracted using MP-RAGE sequence with the following parameters: repetition time (TR) = 2530 ms; echo time (TE) = 2.98 ms; multi-band factor = 2; flip angle = 7 degree; field-of-view (FOV) = $224 \times 256\ \text{mm}^2$; slices = 192; voxel size = $0.5 \times 0.5 \times 1.0\ \text{mm}^3$.

Structural MRI preprocessing

Structural MRI data were preprocessed using the Oxford Centre for Functional MRI of the Brain Software Library voxel-based morphometry (FSL-VBM), a VBM style analysis toolbox implemented in FSL (version 6.0.0; part of the FSL package; http://www.fmrib.ox.ac.uk/fsl). Structural images of brains were extracted, tissue-type segmented, and then aligned to the grey matter template in the MNI152 standard space. The spatially normalized images were averaged to create a study-custom template and the native grey matter images were registered again using both linear and non-linear algorithms. The registered partial volume images were modulated by dividing them with the Jacobian of the warp field to correct for local expansion or contraction. The modulated segmented images, which represented GMV, were smoothed with an isotropic Gaussian kernel with 3 mm standard deviation.

Data analysis

First, bivariate correlational analyses were conducted to examine basic associations between the features related to GPT in both datasets. Linear regression analyses were employed to validate these significant associations controlling for relevant covariates (e.g. parental education, age and sex) partially due to their correlations with GPT in the current study and previous literatures (Liu *et al.*, 2019; Jiang *et al.*, 2020). Significant findings reported in the main text were robust after controlling for covariates and thus are not presented again.

Second, mediation models were run to examine whether negative psychopathology and happiness mediated the effects of GPT on aggression behaviors. Linear regression analysis was used to test the relation between (1) GPT and aggression behaviors ($Y = a_1 + b_1X + \varepsilon_1$); (2) GPT and negative psychopathology/happiness ($M = a_2 + b_2X + \varepsilon_2$); (3) GPT and aggression behaviors with a mediator ($Y = a_3 + b_3X + bM + \varepsilon_3$). In these equations, Y represents the criterion variable, X the predictor variable, and M the mediator. The indirect effect was estimated as $b_2 \times b$ and the bootstrap estimations (1000 resamples) were performed by using SPSS PROCESS v2.16.3 (Version 25.0) (Hayes, 2017) to obtain accurate statistical significance. Due to limited space, we provide the mediation-effect-related figures from the larger dataset but not the smaller dataset.

Third, two EFAs were conducted on the subscales related to GPT using SPSS (version 25.0): one on all the 411 participants and another on the 330 participants with high-quality imaging data. Varimax with Kaiser Normalization was employed to rotate the loading matrix, and regression analysis was used to calculate factor scores from each subscale.

Finally, we examined associations between the factors (i.e. negative psychopathology and happiness) and GMV at the whole-brain level using a mixed-effect FLAME 1 model implemented in FSL. Parental education, age at MRI scans, sex and total GMV were included as covariates. In the regression analyses, covariates were entered into the first block of variables. In the second block, mean-centered factor scores were entered. Statistical results were determined at a cluster level ($z > 2.3$, $P < 0.01$) and at family-wise error rate of 0.05 for the correction for multiple comparisons using Gaussian Random Field Theory (Wang *et al.*, 2019b, 2020, 2021b).

Table 1. Sample demographics

Measures	Dataset 1 ($n = 411$)	Dataset 2 ($n = 68$)	t/X^2	P
Gender (Male/Female)	140/271	30/38	2.576	0.108
Age ($M \pm SD$)	19.93 ± 1.47	20.72 ± 1.74	–3.979	$8.0e^{-5}$
Paternal education (%)			3.563	0.614
Less than primary school	12.7	13.0		
Junior high school	38.2	42.0		
Vocational high School	16.1	17.4		
Senior high school	11.2	13.0		
Junior college education	9.0	2.9		
Undergraduate level	12.9	10.1		
Maternal education (%)			9.672	0.085
Less than primary school	17.0	24.6		
Junior high school	36.0	42.0		
Vocational high school	14.6	4.3		
Senior high school	12.9	11.6		
Junior college education	10.0	4.3		
Undergraduate level	9.4	11.6		

Abbreviations: M, mean score; SD, standard deviation.

Table 2. Basic questionnaires' scores

Measures	Dataset 1($n = 411$)	Dataset 2 ($n = 68$)	t	P
DGS	22.97 ± 4.15	23.29 ± 4.33	–0.595	0.552
SWLS	18.67 ± 5.79	18.06 ± 6.69	0.707	0.482
MASQ				
Mixed symptoms	35.47 ± 9.72	35.37 ± 10.92	0.077	0.939
Depressive	25.03 ± 11.16	22.24 ± 9.14	1.961	0.050
Anxious symptoms	20.67 ± 8.85	16.50 ± 6.63	4.556	$1.3e^{-5}$
Loss of interest	18.35 ± 6.15	17.03 ± 6.67	1.623	0.105
Anxious arousal	28.97 ± 9.27	23.68 ± 6.62	5.731	$8.09e^{-8}$
High positive affect	57.36 ± 21.49	63.82 ± 19.42	–2.329	0.020
SHS	19.11 ± 4.90	18.54 ± 5.58	0.859	0.391
PWBS				
Positive relations	58.86 ± 9.31	58.34 ± 10.05	0.420	0.675
Autonomy	51.74 ± 8.15	51.09 ± 9.08	0.601	0.548
Environmental mastery	54.55 ± 8.26	53.91 ± 9.80	0.512	0.610
Personal growth	60.91 ± 7.86	59.60 ± 7.65	1.274	0.203
Purpose in life	57.58 ± 9.85	56.59 ± 10.26	0.762	0.446
Self-acceptance	52.14 ± 9.33	56.59 ± 10.48	–0.363	0.716
BDI	9.05 ± 9.21	8.90 ± 7.59	0.147	0.883
PANAS				
Positive affect	27.67 ± 7.73	25.81 ± 8.09	1.826	0.068
Negative affect	16.94 ± 6.21	15.97 ± 5.63	1.203	0.230
WPI				
Enjoy	13.89 ± 6.71	13.71 ± 5.92	0.211	0.833
Challenge	–0.23 ± 4.68	0.18 ± 4.54	–0.668	0.504
Outward	7.64 ± 5.32	7.54 ± 4.72	0.136	0.892
Compensation	4.39 ± 3.99	4.43 ± 3.34	–0.077	0.938
Intrinsic	13.66 ± 9.52	13.88 ± 8.31	–0.183	0.855
Extrinsic	12.02 ± 7.49	11.97 ± 6.68	0.056	0.956
BWAQ				
Physical	16.61 ± 5.82	16.57 ± 5.11	0.043	0.966
Verbal	12.84 ± 3.27	12.01 ± 3.05	1.939	0.053
Anger	16.18 ± 4.01	16.07 ± 3.92	0.194	0.846
Hostility	20.51 ± 4.89	20.38 ± 5.14	0.203	0.839
Indirect	14.22 ± 3.88	13.79 ± 3.83	0.838	0.403
Total score	80.35 ± 17.08	78.84 ± 17.12	0.676	0.499
RPQ				
Reactive aggression	6.07 ± 4.13	6.96 ± 3.42	–1.922	0.057
Proactive aggression	0.71 ± 1.82	0.51 ± 1.31	0.830	0.407
SWBS	72.78 ± 11.39	72.93 ± 13.05	0.250	0.803

Results

Demographics

Tables 1 and 2 provide demographic information, each scale's scores in both datasets, and their group comparisons. Minimal significant group differences were found between the two datasets, pertaining only to age ($t_{(477)} = –3.979$, $P < 0.001$), anxious symptoms ($t_{(477)} = 4.556$, $P < 0.001$), anxious arousal, ($t_{(477)} = 5.731$, $P < 0.001$) and high positive affect ($t_{(477)} = –2.329$, $P = 0.020$), suggesting that these two groups were closely homogeneous as a whole and valid for cross-validation. In the first dataset ($n = 411$), the GPT scores ranged from 7 to 35 ($M \pm SD = 22.97 \pm 4.15$) with gender differences ($t_{(409)} = 2.48$, $P = 0.013$). GPT did not vary by age ($r = –0.053$, $P = 0.286$) or maternal education level ($r = 0.064$, $P = 0.199$), but was weakly associated with paternal education level ($r = 0.132$, $P = 0.007$). In the second validation dataset ($n = 68$), the $M \pm SD$ of GPT were 23.30 ± 4.370. Gender differences were not observed in GPT ($t_{(66)} = –0.494$, $P = 0.623$) and GPT was not correlated with age ($r = 0.157$, $P = 0.201$), maternal education level ($r = –0.132$, $P = 0.285$), or paternal education level ($r = –0.234$, $P = 0.055$). Due to non-normal distributions of the raw GPT scores, we used a rank-based inverse Gaussian transformation to convert the GPT scores (Wang *et al.*, 2019a). All findings remained robust to the GPT score transformation except for paternal education level that became significantly associated with GPT in the second dataset, albeit the associated change was minimal (i.e. P value from 0.055 to 0.039). All subsequent analyses were thus conducted using the transformed GPT scores.

Test of common method bias

Prior to formal analysis, we first examined whether the results were influenced by common method bias using the Harman's single-factor test (Podsakoff *et al.*, 2003). This test indicated that the variance explained by the first factor was below the critical 40% threshold (unrotated factor solution: 36.30%; rotated factor solution: 22.27%) in the first dataset and the critical 50% threshold (unrotated factor solution: 43.46%; rotated factor solution: 26.77%) in the second dataset. Both these findings suggest non-significant common method bias effect within these two datasets (Hair, 2009).

GPT's association with greater negative emotions

Table 3 provides correlation results between GPT and the variables of interest. Pertaining to MASQ, GPT was positively correlated with depressive symptoms ($r = 0.156$, $P = 0.001$), anxious symptoms ($r = 0.125$, $P = 0.011$), mixed symptoms ($r = 0.178$, $P < 0.001$) and loss of interest ($r = 0.143$, $P = 0.004$) in the first dataset. These associations were replicated in the second dataset (depressive symptoms: $r = 0.341$, $P = 0.004$; mixed symptoms: $r = 0.482$, $P < 0.001$; loss of interest: $r = 0.323$, $P = 0.007$) except for anxious symptoms ($r = 0.229$, $P = 0.061$). Anxious arousal showed no associations with GPT in either datasets (all Pvalues > 0.054). High positive affect was negatively correlated with GPT in the second ($r = –0.275$, $P = 0.023$) but not in the first dataset ($r = –0.020$, $P = 0.686$).

Table 3. Pearson's correlation coefficients with GPT scores

			Dataset 1 ($n = 411$)		Dataset 2 ($n = 68$)	
GPT			r	P	r	P
Emotion	MASQ	Mixed symptoms	**0.178**	**$2.86e^{-4}$**	**0.482**	**$3.1e^{-5}$**
		Depressive symptoms	**0.156**	**0.001**	**0.341**	**0.004**
		Anxious symptoms	0.125	0.011	0.229	0.061
		Loss of interest	**0.143**	**0.004**	**0.323**	**0.007**
		Anxious arousal	0.021	0.673	0.235	0.054
		High positive affect	−0.020	0.686	−0.275	0.023
	BDI	BDI	**0.141**	**0.004**	**0.320**	**0.008**
	BAI	BAI	0.108	0.028	0.147	0.231
	PANAS	Positive affect	−0.019	0.708	−0.227	0.063
		Negative affect	**0.150**	**0.002**	**0.364**	**0.002**
Happiness	SHS	SHS	−0.104	0.035	−0.195	0.110
	SWBS	SWBS	−0.059	0.233	−0.087	0.478
	PWBS	Positive relations	**−0.163**	**0.001**	**−0.398**	**0.001**
		Autonomy	**−0.110**	**0.026**	**−0.401**	**0.001**
		Environmental mastery	**−0.126**	**0.010**	**−0.338**	**0.005**
		Personal growth	**−0.185**	**$1.62\ e^{-4}$**	**−0.349**	**0.004**
		Purpose in life	**−0.187**	**$1.35\ e^{-4}$**	**−0.380**	**0.001**
		Self-acceptance	**−0.205**	**$2.9\ e^{-5}$**	**−0.367**	**0.002**
Aggression	BWAQ	Physical aggression	**0.211**	**$1.6\ e^{-5}$**	**0.273**	**0.025**
		Verbal aggression	**0.198**	**$5.5\ e^{-5}$**	**0.316**	**0.009**
		Anger	**0.182**	**$2.13\ e^{-4}$**	**0.421**	**$3.54\ e^{-4}$**
		Hostility	**0.329**	**$7.29e^{-12}$**	**0.495**	**$1.7\ e^{-5}$**
		Indirect aggression	**0.197**	**$5.9\ e^{-5}$**	**0.419**	**$3.80\ e^{-4}$**
		Total aggression	**0.291**	**$1.74e^{-9}$**	**0.476**	**$4.0\ e^{-5}$**
	RPQ	Reactive aggression	**0.202**	**$3.7\ e^{-5}$**	**0.316**	**0.009**
		Proactive aggression	0.128	0.01	0.222	0.068
Motivation	WPI	Enjoy	−0.072	0.146	−0.157	0.202
		Challenge	**−0.097**	**0.050**	**−0.363**	**0.002**
		Outward	**0.154**	**0.002**	**0.288**	**0.017**
		Compensation	0.131	0.008	0.004	0.976
		Intrinsic motivation	**−0.098**	**0.047**	**−0.292**	**0.016**
		Extrinsic motivation	0.179	$2.67e^{-4}$	0.206	0.092

Notes: Bold represents significant correlations between GPT and sub-dimensions of scales in both two datasets.

In investigating GPT's associations with depression and anxiety, GPT was positively correlated with depression in both first (depression, $r = 0.141$, $P = 0.004$; negative affect, $r = 0.150$, $P = 0.002$) and second (depression, $r = 0.320$, $P = 0.008$; negative affect, $r = 0.364$, $P = 0.002$) dataset. GPT was positively correlated with anxiety in the first dataset ($r = 0.108$, $P = 0.028$) but not in the second dataset ($r = 0.147$, $P = 0.231$). No significant association was observed for positive affect (all P values > 0.063) in either datasets.

Regarding loss of interest, GPT was negatively correlated with the dimensions of challenge (all P values < 0.05) and intrinsic motivation (all P values < 0.05) while positively correlated with the outward motivation dimension (all P values < 0.05) in both datasets. Individuals with higher GPT scores exhibited more compensation ($r = 0.131$, $P = 0.008$) and extrinsic ($r = 0.179$, $P < 0.001$) motivation in the first dataset but not in the second dataset (all P values > 0.092).

GPT's association with lower happiness

Negative associations of GPT with psychological well-being in all sub-scales of the measurements used (details in Table 2) were generally observed across both datasets (Table 3). GPT was negatively correlated with positive relations (all P values < 0.001), autonomy (all P values < 0.05), environment (all P values < 0.05), personal growth (all P values < 0.005), purpose in life (all P values < 0.001) and self-acceptance (all P values < 0.005) in both two datasets. However, a negative association between GPT and subjective happiness was only observed in the first dataset ($r = -0.104$, $P = 0.035$). No any other associations were observed (all P values > 0.1).

GPT's association with greater aggressive behaviors

Pertaining to BWAQ, we observed significant associations of GPT with physical aggression (all P values < 0.05), verbal aggression (all P values < 0.01), anger (all P values < 0.001), hostility (all P values < 0.001), indirect aggression (all P values < 0.001) and aggregate scores (all P values < 0.001) in both two datasets (Table 3). In relation to RPQ, GPT was positively correlated to reactive aggression ($r = 0.202$, $P < 0.001$) and proactive ($r = 0.128$, $P = 0.009$) aggression in the first dataset. We observed a similar pattern in reactive aggression ($r = 0.316$, $P = 0.009$) but only marginal significance in proactive aggression ($r = 0.222$, $P = 0.068$) in the second dataset.

Negative psychopathology symptoms modulate the association between GPT and aggression

Mixed symptom mediated the effects of GPT on physical aggression, anger, hostility and aggregate aggression score in BWAQ

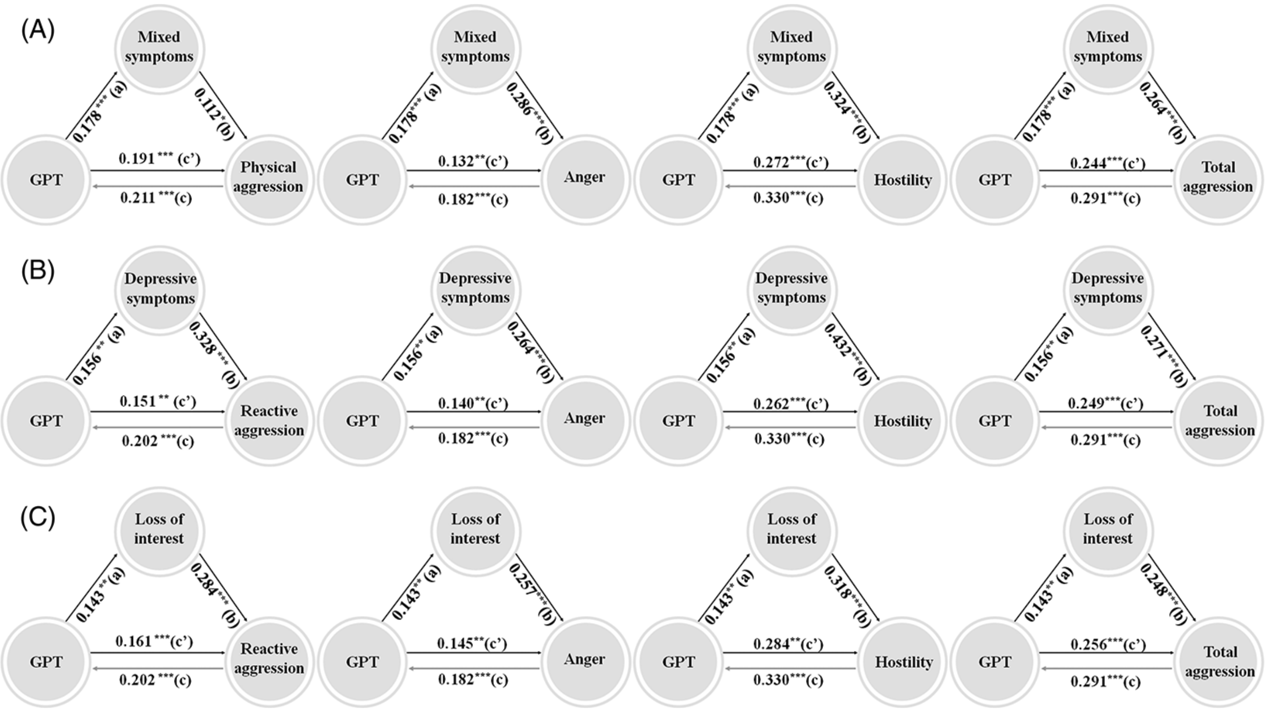

Fig. 1. Mediation models of negative symptoms (including depressive symptoms (A), mixed symptoms (B) and loss of interest (C)) on the relationships between GPT and aggression behaviors (including the reactive, physical, anger, hostility and total scores of BWAQ).

(Figure 1A). In particular, mixed symptoms respectively partially and fully mediated the associations between GPT and physical aggression in the first (indirect effect = 0.020, 95% CI [0.003, 0.050]) and second dataset (indirect effect = 0.117, 95% CI [0.008, 0.298]). In addition, we observed similar mediation effects in anger (all indirect effects > 0.050, 95% CI [0.021, 0.346]) and hostility (all indirect effects > 0.050, 95% CI [0.027, 0.324]), as well as aggregate aggression scores (all indirect effects > 0.045, 95% CI [0.021, 0.333]).

Depression symptom likewise showed similar mediation effects (Figure 1B). Specifically, depression mediated the effects of GPT on reactive aggression (all indirect effects > 0.051, 95% CI [0.006, 0.206]), anger (all indirect effects > 0.041, 95% CI [0.017, 0.258]), hostility (all indirect effects > 0.067, 95% CI [0.031, 0.257]), as well as aggregate aggression scores of BWAQ (all indirect effects > 0.042, 95% CI [0.014, 0.251]). Moreover, we found the similar mediation effects of depression as measured by BDI on anger (all indirect effects > 0.040, 95% CI [0.015,0.242]), hostility (all indirect effects > 0.060, 95% CI [0.023, 0.288]) and aggregate aggression scores of BWAQ (all indirect effects > 0.037, 95% CI [0.014, 0.224]) (Figure 2B).

Thirdly, pertaining to the loss of interest subdimension, we observed similar mediation effects as depression (Figure 1C). Mediation analyses revealed that loss of interest mediated the underlying effects of GPT on reactive aggression in RPQ (all indirect effects > 0.041, 95% CI [0.001,0.170])), anger (all indirect effects > 0.037, 95% CI [0.013, 0.238]) and hostility (all indirect effects > 0.046, 95% CI [0.017, 0.249]).

In addition, we found that negative affect mediated more GPT effects on aggression (i.e. reactive aggression, physical aggression, anger, hostility and indirect aggression) than the aforementioned mediator variables (Figure 2A). Paritcularly, negative affect mediated the effects of GPT on reactive aggression (all indirect effects > 0.054, 95% CI [0.021, 0.241]), physical aggression (all indirect effects > 0.033, 95% CI [0.012, 0.235]), anger (all indirect effects > 0.049, 95% CI [0.018, 0.334], hostility (all indirect effects > 0.060, 95%CI [0.025, 0.350]), indirect aggression (all indirect effects > 0.036, 95% CI [0.013, 0.292]) and aggregate scores of BWAQ (all indirect effects > 0.054, 95% CI [0.022,0.341]) across both datasets.

Psychological well-being modulates the associations between GPT and aggression

Pertaining to reactive aggression (RPQ) and physical aggression (BWAQ), we observed significant mediating roles of purpose in life, a sub-dimension of psychological well-being, on the effect of GPT in both datasets (For reactive aggression, all indirect effects > 0.020, 95% CI [0.002, 0.188]; For physical aggression, all indirect effects > 0.040, 95% CI [0.001, 0.193]) (Figure 3D).

Secondly, for anger (BWAQ), nearly all sub-dimensions of PWBS mediated the effect of GPT, except for autonomy (Figure 3A). Specifically, the mediation effects were significant for positive relations (all indirect effects > 0.039, 95% CI [0.015, 0.308]), environmental mastery (all indirect effects > 0.039, 95% CI [0.010, 0.328]), personal growth (all indirect effects > 0.052, 95% CI [0.024, 0.296]), purpose in life (all indirect effects > 0.054, 95% CI [0.025, 0.331]), and self-acceptance (all indirect effects > 0.052, 95% CI [0.025, 0.313]).

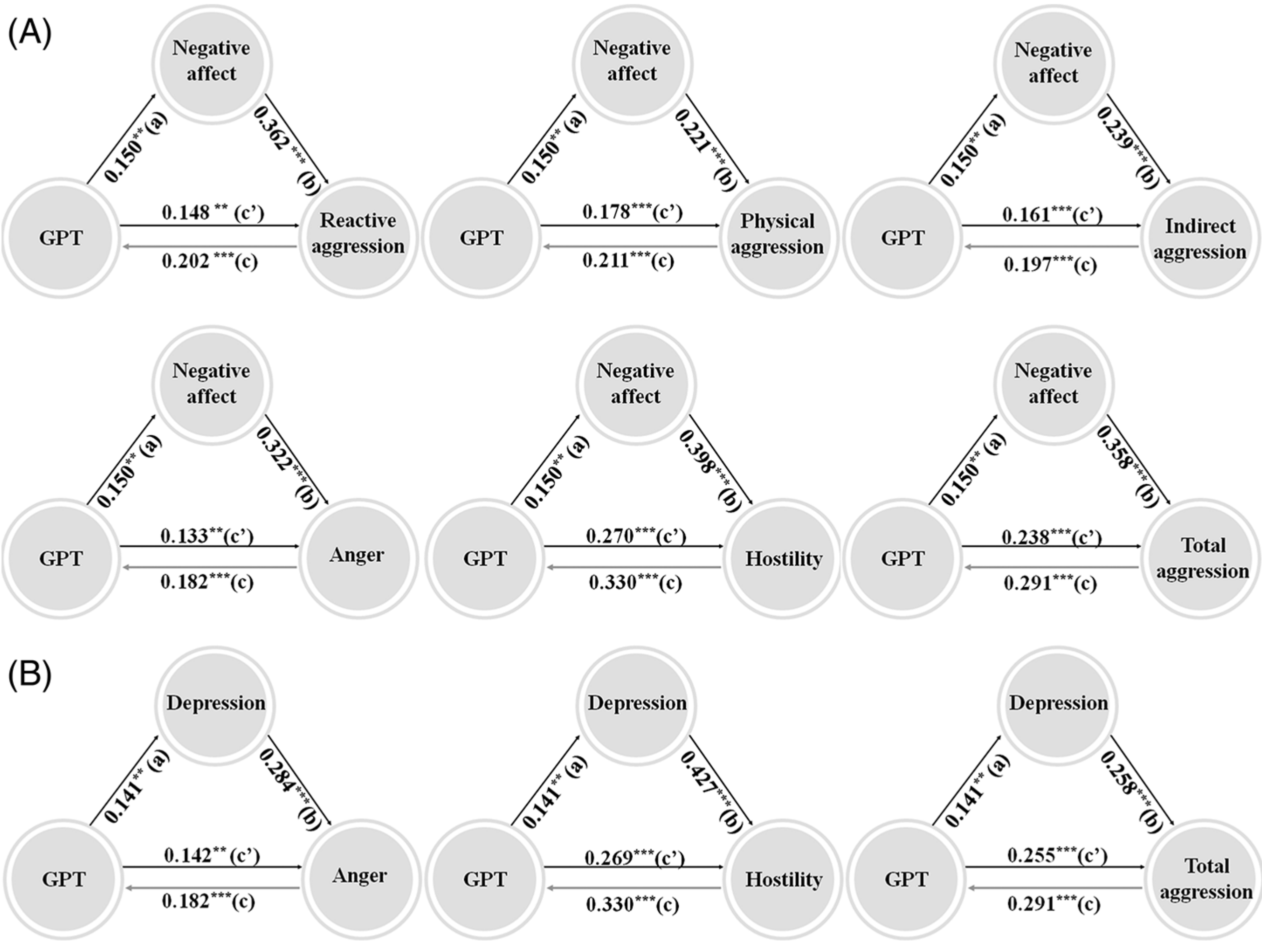

Fig. 2. Mediation models of negative affect and depression on the associations between GPT and aggression (including reactive aggression, physical, indirect, anger, hostility, total aggression of BWAQ).

Thirdly, for hostility (BWAQ), we likewise observed that all sub-dimensions of PWBS served as mediators in both datasets (Figure 3B). Specifically, the mediation effects were significant for positive relations (all indirect effects > 0.056, 95% CI [0.023, 0.370]), autonomy (all indirect effects > 0.031, 95% CI [0.001,0.342]), environmental mastery (all indirect effects > 0.049, 95% CI [0.013, 0.334]), personal growth (all indirect effects > 0.045, 95% CI [0.021, 0.280]), purpose in life (all indirect effects > 0.064, 95% CI [0.029, 0.344]) and self-acceptance (all indirect effects > 0.092, 95% CI [0.052, 0.393]).

Fourthly, for indirect aggression (BWAQ), we found that only environmental mastery (all indirect effects > 0.022, 95% CI [0.005, 0.271]) and purpose in life (all indirect effects > 0.027, 95% CI [0.007, 0,305]) exhibited significantly partial mediation effects on the effect of GPT (Figure 3E).

Finally, for the aggregate scores of aggression in the BWAQ, almost all sub-dimensions of PWBS exhibited the mediation effects on the associations between it and GPT (Figure 3C). Specifically, mediation effects were found for positive relations (all indirect effects > 0.043, 95% CI [0.017, 0.272]), environmental mastery (all indirect effects > 0.036, 95% CI [0.009, 0.290]), personal growth (all indirect effects > 0.040, 95% CI [0.017, 0.256]), purpose in life (all indirect effects > 0.059, 95% CI [0.027, 0.303]) and self-acceptance (all indirect effects > 0.051, 95% CI [0.025, 0.301]) in both datasets.

Three major factors and their relations with GPT

The aforementioned analyses consistently demonstrated the close associations of GPT with negative psychopathology (i.e. mixed, depression symptoms, loss of interest, and negative affect), happiness (i.e. psychological well-being) and motivation. To further investigate patterns of effect, we further extracted the key factors between these measures using EFA for additional analyses.

Bartlett's test of sphericity ($\chi^2 = 3272.42$, $P < 0.001$) and the Kaiser-Meyer-Olkin test (value = 0.88) suggested the data were suitable for EFA. The 13 measures that exhibited significant correlations with GPT and had mediation effects in dataset 1 were entered in the analysis. Three factors were extracted based on the criteria of eigenvalues > 1 and variance explained > 60%: (i) negative psychopathology (fivesubscales), (ii) happiness (six subscales) and (iii) motivation (two subscales), which accounted for 70.74% of the total variance of the items. Table 4 displays the varimax rotated factor loadings greater than 0.40.

We further explored whether such factors remained correlated with GPT and their mediating roles between GPT and aggression were robust (Table 5). Results revealed that the negative psychopathology (factor 1) was positively correlated with GPT ($r = 0.147$, $P = 0.003$), physical ($r = 0.144$, $P = 0.003$), verbal ($r = 0.147$, $P = 0.003$), anger ($r = 0.303$, $P < 0.001$), hostility ($r = 0.456$, $P < 0.001$), indirect ($r = 0.214$, $P < 0.001$), aggreate score of BWAQ

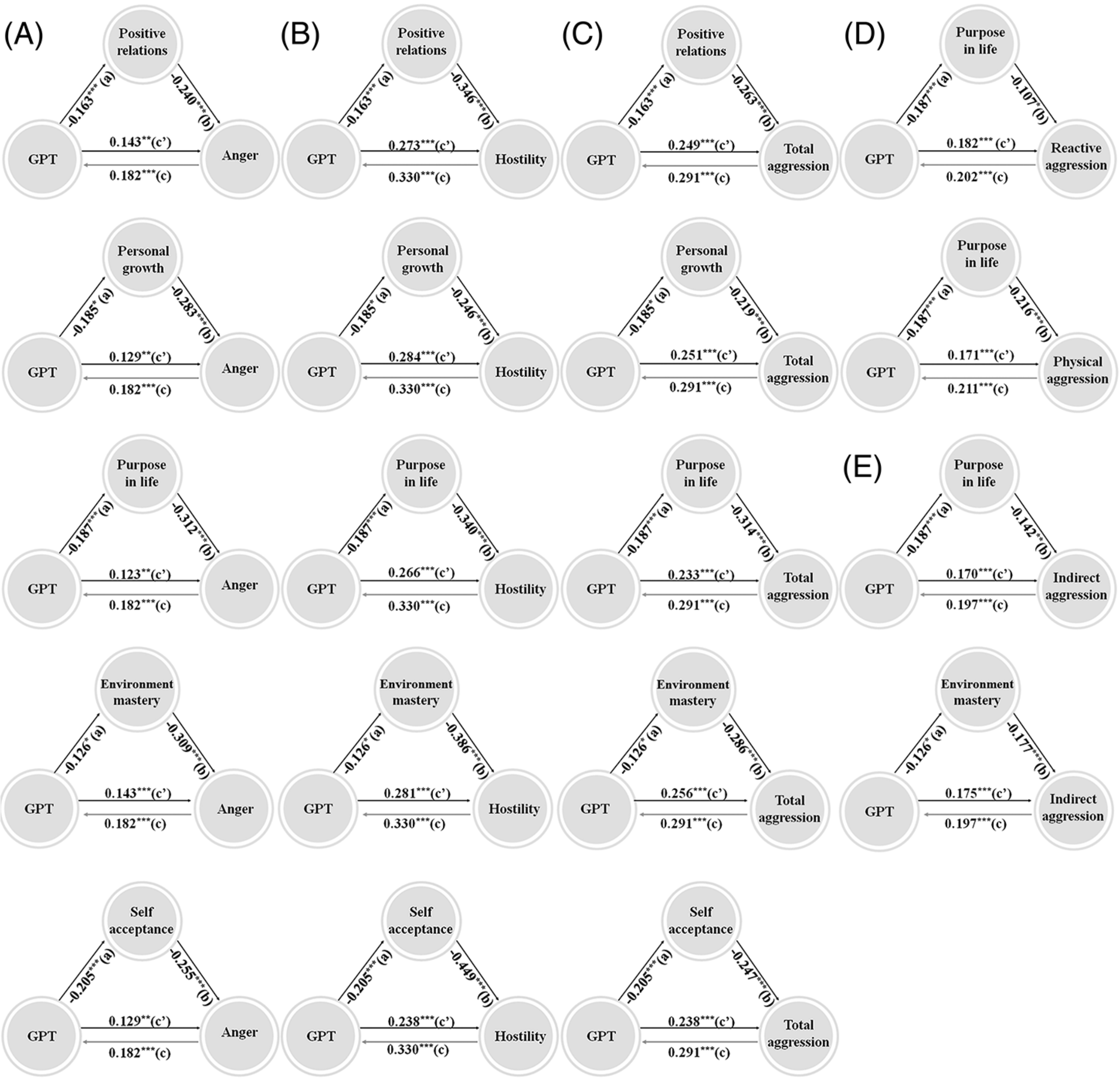

Fig. 3. Mediation models of PWBS sub-dimensions (i.e. positive relations with others, personal growth and self-acceptance) on the associations between GPT and aggression (including anger (A), hostility (B), total aggression of BWAQ (C), reactive/physical aggression (D) and indirect aggression €).

($r = 0.327$, $P < 0.001$), reactive aggression ($r = 0.411$, $P < 0.001$) and proactive aggression ($r = 0.226$, $P < 0.001$) in the first dataset. Additionally, happiness (factor 2) was negatively correlated with GPT ($r = -0.150$, $P = 0.002$), physical ($r = -0.206$, $P < 0.001$), verbal ($r = -0.187$, $P < 0.001$), anger ($r = -0.263$, $P < 0.001$), hostility ($r = -0.311$, $P < 0.001$), aggregate score of BWAQ ($r = -0.276$, $P < 0.001$) and proactive aggression ($r = -0.152$, $P = 0.002$). However, we only observe a few small correlations of motivation (factor 3) with physical aggression ($r = 0.109$, $P = 0.027$), verbal aggression ($r = 0.125$, $P = 0.011$) and hostility ($r = -0.120$, $P = 0.015$) of BWAQ. Overall, these associations were replicated in the subgroup with high-quality imaging scans ($n = 330$) for negative psychopathology and happiness but not motivation (Table 5).

Negative psychopathology and happiness factors correspondingly mediated the effect of GPT on aggression (Figure 4). Negative psychopathology mediated the associations of GPT with physical aggression (all indirect effects > 0.017, 95% CI [0.002, 0.065]), verbal aggression (all indirect effects > 0.018, 95% CI [0.001, 0.063]), anger (all indirect effects > 0.042, 95% CI [0.016, 0.089]), hostility (all indirect effects > 0.061, 95% CI [0.026, 0.111]), indirect aggression (all indirect effects > 0.028, 95% CI [0.008, 0.086]), aggregate scores of BWAQ (all indirect effects > 0.043, 95% CI [0.017, 0.097]) and reactive aggression (all indirect effects > 0.058, 95% CI [0.023, 0.124]). Similarly, happiness mediated GPT effects on physical aggression (all indirect effects > 0.027, 95% CI [0.009, 0.073]), verbal aggression (all indirect effects > 0.024, 95% CI [0.006, 0.075]), anger (all indirect effects > 0.036, 95% CI [0.013, 0.084]), hostility (all indirect effects > 0.040, 95% CI [0.014, 0.099]) and aggregate scores of BWAQ (all indirect effects > 0.036, 95% CI [0.012, 0.086]). These mediation effects were robust in the subgroup with high-quality imaging scans ($n = 330$; all indirect effects > 0.01, 95% CI [0.006,0.124]).

Table 4. Exploratory factor analysis of the 13 subscales revealed three major factors

Sub-dimensions	Negative psychopathology	Happiness	Motivation
Mixed symptoms	0.75		
Depressive symptoms	0.87		
Loss of interest	0.77		
BDI	0.78		
PANAS_NA	0.73		
Positive relations		0.82	
Autonomy		0.42	0.54
Environmental mastery	−0.44	0.74	
Personal growth		0.74	
Purpose in life		0.81	
Self-acceptance	−0.53	0.57	
Challenge			0.92
Intrinsic motivation			0.87

Note: Factor loadings below 0.40 not shown.

The morphological substrates of negative psychopathology and happiness

We further explored whether the mediation effects observed were also associated with brain morphological substrates underlying negative psycholopathology and happiness. First, VBM analysis revealed that negative psychopathology was positively associated with the GMVs in the left precentral gyrus (MNI = −7.25, −25, 74, Z = 3.65), right frontal operculum cortex (MNI = 37.6, 21, 6, Z = 2.98), right precentral gyrus (MNI = 28.9, −14.6, 69.9, Z = 3.42), right LOC (MNI = 17.8, −67.6, 55.8, Z = 3.73), left insular cortex (MNI = −34.4, 22, −6.33, Z = 3.02), left LOC (MNI = -9.62, −61.1,—67.8, Z = 3.55), right superior frontal gyrus (SFG; MNI = 8.08, 2.09, 72.6, Z = 3.13), left middle frontal gyrus (MFG; MNI = −30.7, 2.32, 64, Z = 3.44), left SFG (MNI = −21.4, 17.2, 47.5, Z = 2.51), right superior parietal lobule (SPL; MNI = 12.6, −46.7, 76.4, Z = 3.64), right ventromedial prefrontal cortex (VMPFC; MNI = 0.947, 16.1, 5.51, Z = 3.32) and left frontal orbital cortex (OFC; MNI = −19.3, 33.3, −22.3, Z = 2.73) (Table 6) (Figure 5). Moreover, negative psychopathology was negatively associated with GMVs in the frontal-temporal-occipital network, including the right middle temporal gyrus (MTG; MNI = 50.7, −26.4, −3.95, Z = 3.00), right precuneus cortex (MNI = 19.8, −66.2, 30.5, Z = 3.47), right occipital pole (OP; MNI = 13.1, −96.5, −10.3, Z = 3.27), left frontal pole (FPC; MNI = −34.5, 57.1, −8.66, Z = 3.53), left inferior frontal gyrus (IFG; MNI = −46.1, 31, 18.2, Z = 3.33), left LOC (MNI = −30.2, −79.5, 2.54, Z = 3.19), right OFC (MNI = 13.7, 16.7, −16.4, Z = 2.65), left STG (MNI = −47.8, −0.775, −19.3, Z = 3.13), left MTG (MNI = −33.9, 23.4, 37.3, Z = 4.12) and right MFG (MNI = 39.7, 27.3, 22.7, Z = 2.81) (Table 6) (Figure 5).

In contrast, happiness was positively correlated with GMVs in the left postcentral gyrus (MNI = −10.8, −42.6, 58.3, Z= 2.83), but negatively correlated with GMVs in the prefronal-temporal-occipital-parietal network, including the left temporal pole (TP; MNI = −27.7, 11.7, −38.7, Z = 3.20), left MFG (MNI = -40.1, 24.4, 35.7, Z = 3.37), left lateral occipital pole (LOP; MNI = -35.2, −62.6, 34.8, Z = 4.03), left angular gyrus (MNI = −48.5, −51.1, 34.5, Z = 3.85), left LOC (MNI = −15, −66.4, 50.7, Z = 3.45), left inferior temporal gyrus (ITG; MNI = −48.1, −11, −43.3, Z = 3.03), right LOC (MNI = 42.9, −65.5, 39.8, Z = 2.93), right precentral gyrus (MNI = 56.5, 1.02, 15.7, Z = 2.98), left cingulate gyrus (MNI = −8.78, −49.1, 24.3, Z = 2.88) and right MFG (MNI = 29, 23, 33.1, Z = 2.70) (Table 7) (Figure 5).

We further explored whether the GMVs in above-mentioned brain regions predicted individual variability in GPT and aggression. We found that the negative psychopathology-related FPC's GMV was negatively associated with GPT ($r = -0.132$, $P = 0.017$), reactive aggression ($r = -0.201$, $P < 0.001$) and hostility of BWAQ ($r = -0.152$, $P = 0.006$). Similarly, the happiness-related GMVs in the left MFG ($r = 0.134$, $P = 0.015$), left angular gyrus ($r = 0.136$, $P = 0.013$) and right MFG ($r = 0.114$, $P = 0.039$) were positively associated with GPT. Furthermore, GMVs in the left MFG was positively correlated with physical aggression ($r = 0.128$, $P = 0.02$), while GMVs in the left angular gyrus was positively correlated with hostility aggression ($r = 0.118$, $P = 0.032$). The GMV in right MFG was found to be associated with physical ($r = 0.174$, $P = 0.001$), hostility ($r = 0.145$, $P = 0.009$) and aggregate scores of aggression ($r = 0.146$, $P = 0.008$).

We further examined whether the associations between GPT and aggressions were modulated by the GMVs in above-mentioned brain regions. Mediation models revealed that GMV in the FPC mediated the association between GPT and reactive aggression (indirect effect = 0.012, 95% CI = [0.002, 0.031]). Additionally, MFG's volume mediated greedy individuals' aggressions, including physical (indirect effect = 0.017, 95% CI [0.002, 0.044]), hostility (indirect effect = 0.012, 95% CI [0.000, 0.033]) and aggregate scores of aggression (indirect effect = 0.013, 95% CI [0.001, 0.035]) (Figure 6).

Table 5. Correlations between three major factors and GPT/aggression scores

	Dataset 1 ($n = 411$)			**Sub-dataset 1 ($n = 330$)**		
Measures	**F1**	**F2**	**F3**	**F1**	**F2**	**F3**
GPT	0.147**	−0.150**	−0.066	0.178**	−0.182**	−0.107
Physical	0.144**	−0.206***	0.109*	0.184**	−0.232***	0.096
Verbal	0.147**	−0.187***	0.125*	0.183**	−0.224***	0.108
Anger	0.303***	−0.263***	−0.071	0.305***	−0.264***	−0.049
Hostility	0.456***	−0.311***	−0.120*	0.434***	−0.362***	−0.067
Indirect	0.214***	−0.084	0.009	0.253***	−0.066	0.016
Total aggression	0.327***	−0.276***	0.012	0.348***	−0.300***	0.026
Reactive aggression	0.411***	−0.062	−0.028	0.441***	−0.095	0.038
Proactive aggression	0.226***	−0.152**	−0.014	0.297***	−0.172**	−0.012

Abbreviations: F1, negative psychopathology; F2, happiness; F3, motivation. $^{*}P < 0.05$;
$^{**}P < 0.01$;
$^{***}P < 0.001$.

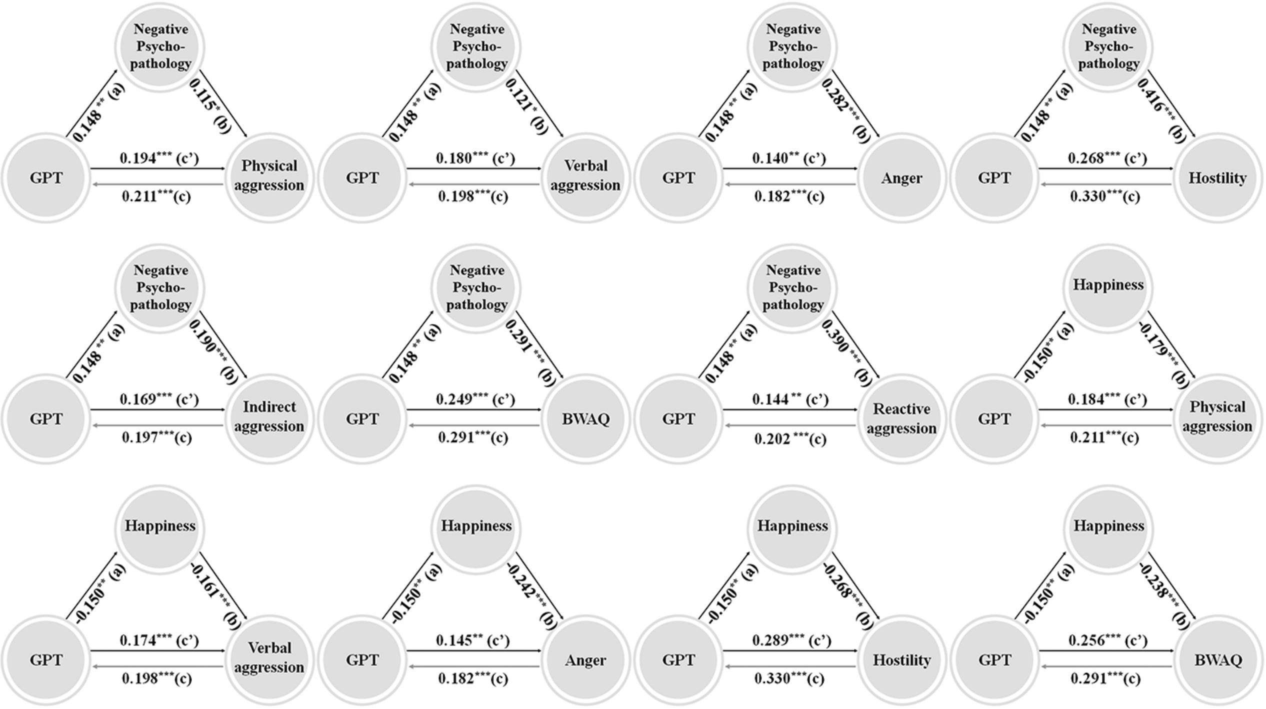

Fig. 4. Mediation models of two factors (i.e. negative psychopathology and happiness) on relationships between GPT and aggressions (including physical, verbal, anger, hostility, indirect, total scores of BWAQ, reactive aggression).

Table 6. Statistical associations between GMVs and negative psychopathology

			MNI coordinates			
Effect	**Brain region**	**Cluster size (voxels)**	**X**	**Y**	**Z**	**Z**
Positive	L Precentral Gyrus	810	−7.25	−25	74	3.65
	R Frontal Operculum Cortex	742	37.6	21	6	2.98
	R Precentral Gyrus	701	28.9	−14.6	69.9	3.42
	R Lateral Occipital Cortex	625	17.8	−67.6	55.8	3.73
	L Insular Cortex	451	−34.4	22	−6.33	3.02
	L Lateral Occipital Cortex	338	−9.62	−61.1	67.8	3.55
	R Superior Frontal Gyrus	297	8.08	2.09	72.6	3.13
	L Middle Frontal Gyrus	285	−30.7	2.32	64	3.44
	L Superior Frontal Gyrus	223	−21.4	17.2	47.5	2.51
	R Superior Parietal Lobule	156	12.6	−46.7	76.4	3.64
	R VMPFC	136	0.947	16.1	5.51	3.32
	L Frontal Orbital Cortex	114	−19.3	33.3	−22.3	2.73
Negative	R Middle Temporal Gyrus	1085	50.7	−26.4	−3.95	3.00
	R Precuneus Cortex	983	19.8	−66.2	30.5	3.47
	R Occipital Pole	683	13.1	−96.5	−10.3	3.27
	L Frontal Pole	634	−34.5	57.1	−8.66	3.53
	L Inferior Frontal Gyrus	468	−46.1	31	18.2	3.33
	L Lateral Occipital Cortex	249	−30.2	−79.5	2.54	3.19
	R Frontal Orbital Cortex	205	13.7	16.7	−16.4	2.65
	L Superior Temporal Gyrus	205	−47.8	−0.775	−19.3	3.13
	L Middle Temporal Gyrus	143	−33.9	23.4	37.3	4.12
	R Middle Frontal Gyrus	127	39.7	27.3	22.7	2.81

Notes: Positive and Negative represents positive and negative associations between GMVs and negative psychopathology.

Discussion

The present study comprehensively examined negative psychopathological symptomology as direct correlates and mediating mechanisms of dispositional greed (e.g. depression, mixed symptoms, loss of interest, negative affect) on its relation to maladaptive social behaviors (e.g. aggression). Further, EFA generated three factors, including negative psychopathology, happiness and motivation, two of which functioned as mediators. Brain imaging findings further revealed the neuroanatomical characteristics of negative psychopathology and happiness for the GMVs in the prefrontal-parietal-occipital system. Moreover, we found that behavioral mediation effects on the associations between greed

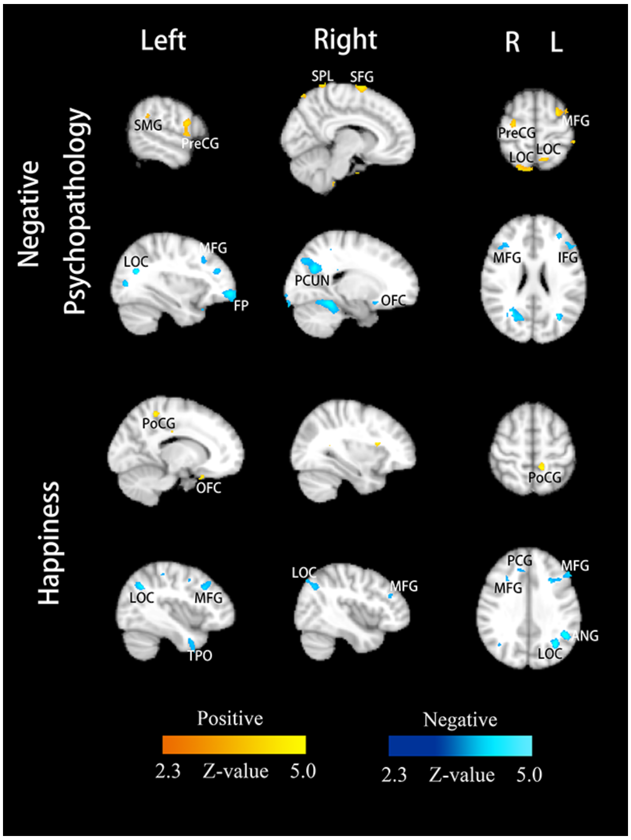

Fig. 5. Gray matter volume's results related to negative psychophology and happiness.

and aggression depended on the brain morphological architecture, particularly the negative-feature-related FPC and happiness-trait-related MFG volumes. This situates the current work as one of the first to comprehensively delineate behavioral characteristics in relation to greed, and its potential mediating and neuroanatomical mechanisms, with particular focus on the prefrontal cortex.

Utilizing the MASQ as the initial exploratory step revealed notable associations between GPT and psychopathological symptomology, such as depression symptoms, mixed symptoms and loss of interest. To further validate these findings, we utilized other field-standard measures (i.e. BDI and BAI) to isolate depression and anxiety symptomology, showing evidence greedy individuals tended to exhibit more depression-related psychopathology. Further, using PANAS as a general proxy for affective states likewise observed a positive correlation between GPT and negative affect. Importantly, such core outcomes were also replicated in an independent dataset, implying the robust nature and co-occurrence of adverse affective experiences and negative psychopathology among greedy individuals. Our findings are largely consistent with past studies that have found similar negative behavioral and psychological consequences among greedy individuals across both directly and peripherally related domains, including increased envy (Winarick, 2010), low life satisfaction (Krekels and Pandelaere, 2015), disrupted impression management (Krekels and Pandelaere, 2015), adverse financial behavior (Seuntjens *et al.*, 2016) and increased likelihood to accept bribes (Seuntjens *et al.*, 2019). One potential reason for GPT's association with negative emotion/affect may be due to pervasive upward social comparison caused by materialistic desire to have more (Balot, 2020). This long-term state of dissatisfaction and corresponding desire for an idealistic, yet likely unattainable lifestyle may further induce the loss of interest with one's current environment, thereby manifesting as psychopathological symptomology (e.g. depression, anxiety and mixed symptoms).

The present study also investigated the relation between greed and different aspects of social aggression, including reactivity, physical aggression, anger, hostility and indirect aggression. Negative psychopathological symptomology mediated the effect of greed on aggression. Specifically, the two main factors extracted by EFA, i.e. negative psychopathology and happiness, validated these mediation effects. This suggests the importance of negative psychopathological symptomology on the explanation of greed's psychological and social consequences. Indeed, several studies have likewise implied the influence of negative emotion and affect on aggression. Negative emotions triggered by exposure to averse situations were found to modulate aggressive behavior, suggesting an affective priming effect on aggression (Verona *et al.*, 2002). In adolescents, the level of the daily negative emotions, such as anger, was associated with reactive aggression (Moore *et al.*, 2019). On the other hand, positive emotions, such as happiness, have been associated with lower physical aggression (Ronen *et al.*, 2013; Kılıçarslan and Liman, 2020). Taken together, greedy individuals may be more prone to aggress against others due to higher

Table 7. Statistical associations between GMVs and happiness

			MNI Coordinates			
Effect	**Brain Region**	**Cluster size (voxels)**	**X**	**Y**	**Z**	**Z**
Positive	L Postcentral Gyrus	134	−10.8	−42.6	58.3	2.83
Negative	L Temporal Pole	1015	−27.7	11.7	−38.7	3.20
	L Middle Frontal Gyrus	668	−40.1	24.4	35.7	3.37
	L Lateral Occipital Pole	330	−35.2	−62.6	34.8	4.03
	L Angular Gyrus	311	−48.5	−51.1	34.5	3.85
	L Lateral Occipital Cortex	300	−15	−66.4	50.7	3.45
	L Inferior Temporal Gyrus	261	−48.1	−11	−43.3	3.03
	R Lateral Occipital Cortex	255	42.9	−65.5	39.8	2.93
	R Precentral Gyrus	174	56.5	1.02	15.7	2.98
	L Cingulate Gyrus	129	−8.78	−49.1	24.3	2.88
	R Middle Frontal Gyrus	35	29	23	33.1	2.70

Notes: Positive and Negative represents positive and negative associations between GMVs and happiness.

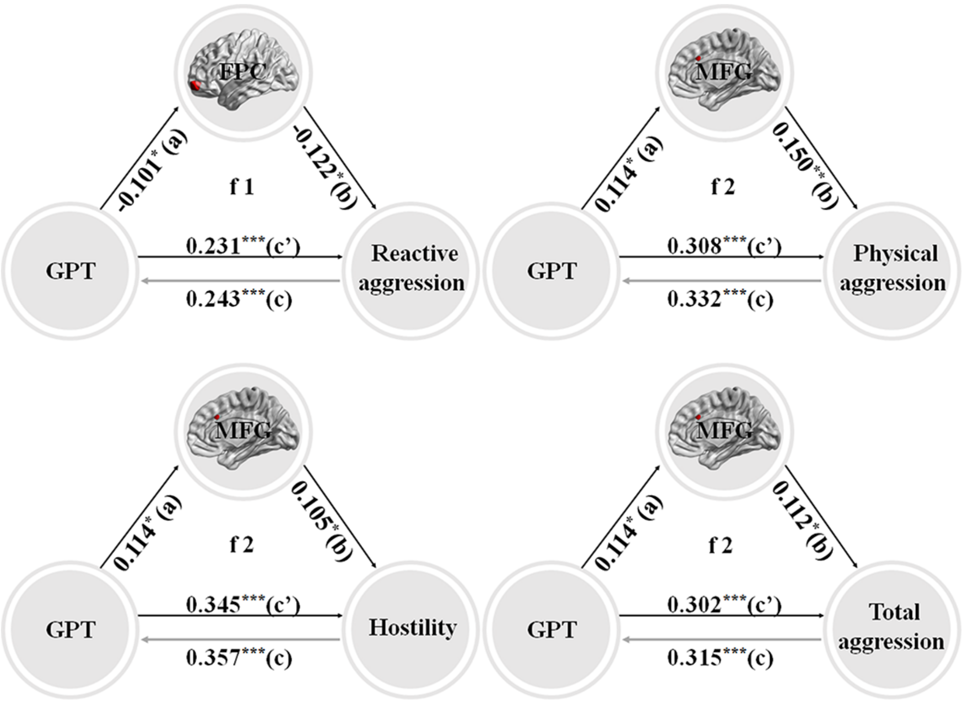

Fig. 6. Mediation models of brain regions on associations between GPT and aggression (FPC: Frontal Pole Cortex; MEG: Middle Frontal Gyrus).

experience of negative emotions and low happiness stemming from pervasive dissatisfaction of not having enough.

EFA further revealed that there are three main latent constructs of negative psychopathology, happiness, and motivation, of which two revealed significant mediation effects of greed on aggression. Furthermore, VBM analysis showed the neuroanatomical substrates underlying negative psychopathology and happiness in the prefrontal-parietal-temporal-occipital system. In particular, the GMVs in the prefrontal-parietal network, including DLPFC, SPL, VMPFC, MFG, OFC and IFG, were associated with individual variability in negative psychopathology scores assessed by EFA, consistent with previous studies focusing on the neuroanatomical substrates of negative emotion and affect. Specifically, anxious/depressed symptoms were linked to the thickness in VMPFC and exhibited developmental characteristics (Ducharme *et al.*, 2014; Newman *et al.*, 2016). GMVs in cortical and subcortical cortices, including VMPFC, MPFC, ACC, IFG, insula and amygdala-hippocampus were found to be important for emotion and relevant regulation (Koven *et al.*, 2010; Takeuchi *et al.*, 2011; Killgore *et al.*, 2012). Meta-analyses on neuroimaging studies have found that emotion-regulation (e.g. reappraisal) relies on several brain activations, including DLPFC, ventrolateral PFC, DMPFC, ACC and the parietal cortex (Kohn *et al.*, 2014; Etkin *et al.*, 2015), to decrease amygdala-related emotion brain activations. Moreover, Beck's cognitive model of depression proposed that the functional and structural architectures on the aforementioned prefrontal cortices are the core brain regions that play critical roles on depression formation, including the modulation of the subcortical brain activations subserving into negative emotion processing, top-down cognitive control, and attention bias modification (Disner *et al.*, 2011). Youths with bipolar disorder also exhibited specific GMV decreases in the lateral PFC, DLPFC, DMPFC and parahippocampal gyrus (Gold *et al.*, 2016). Thus, the subcortical region, with particular emphasis on the amygdala, may hint at a potential top-down cognitive control processing important on negative psychopathology.

We also found that GMVs in negative-psychopathology-related FPC and happiness-related MFG could modulate the effects of greed on aggression, which further extends the neurobiological architecture of behavioral mediation effects and suggests that morphological organization might exert a critical role between greed and aggression. A recent study showed that the GMVs in the FPC were directly associated with individual variability in GPT (Wang *et al.*, 2021a). Importantly, reward-related brain activations in the lateral OFC and prospective-thinking-related brain activations in the prefrontal network, including MFG, significantly predicted individual's GPT scores (Wang *et al.*, 2021a). Combining the functioning of these regions, we propose that negative psychopathology may modulate greed-related effects on aggression and this modulation effect may correspondingly depend on the prefrontal cortex morphological characteristics.

From the theoretical perspective, the current study not only directly examined the negative psychopathology core characteristics of greed possibly due to desiring more than normal need and the dissatisfaction of not have enough, but also further uncovered its adverse consequences on social behaviors (e.g. aggression) and potential neural substrates. Such findings further extend the understanding of the negative attributes of greed from traditional self-interest, materialism and maximization to negative emotion/affect and maladaptive social behaviors to neural mechanisms(Krekels and Pandelaere, 2015; Seuntjens *et al.*, 2015b; Lambie and Haugen, 2019). It enables us to comprehensively and precisely understand the concept of greed from a theoretical view. At the practical level, it provides the possible strategies that focus on the emotion/affect-related manipulations and enhancements to further improve the life quality for greedy individuals. In addition, the current study is also valuable for shaping the economic behaviors in childhood and government management.

There are several limitations to consider in the present study. All findings of this study stem from a correlational design and do not allow for causal relations. Future studies may use experimental or longitudinal designs to examine the robustness of the current findings. Second, the behavioral data in this study were collected through self-report questionnaires which are subject to social desirability bias. Nonetheless, an independent sample provided consistent validation, increasing our confidence on the research conclusions. Third, the sample consisted of university students which may limit the extent to which these findings can be generalized to other populations. In addition, the morphological findings related to two main factors via EFA and mediation model cannot tell us specific functions and warrant further inquiry to understand the functional mechanisms of greed and its mediators on greed-aggression associations.

In conclusion, the present study systematically investigated the negative characteristics of dispositional greed and its relation to aggression, as well as its underlying neuroanatomical substrates. Our findings provided empirical evidence on greed-aggression association and observed that negative psychopathology, happiness, and GMVs in prefrontal cortex could mediate such associations. These findings improve our understanding of greed and the cognitive and neural mechanisms that may underly its role in behavioral aggression.

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Conflict of interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

Research involving human participants

Ethnical approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the Institutional Review Board (IRB) of the Tianjin Normal University and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all participants included in the study.

Informed consent

Informed consent was obtained from all individual participants included in the study.

Data and code availability

The data that support the findings of this study are available from the Functional MRI Center at Tianjin Normal University (TJNU). Data and code are available from the corresponding authors with the permission of the TJNU.

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