Neuroanatomical and functional substrates of the greed personality trait

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Abstract
Greedy individuals often exhibit more impulsive decision-making and short-sighted behaviors. It has been assumed that altered reward circuitry and prospection network is associated with greed personality trait (GPT). In this study, we first explored the morphological characteristics (i.e., gray matter volume; GMV) of GPT combined with univariate and multivariate pattern analysis (MVPA) approaches. Second, we adopted a revised version of inter-temporal choice task and independently manipulated the amount and delay time of future rewards. Using brain-imaging design, reward- and prospection-related brain activations were assessed and their associations with GPT were further examined. The MVPA results showed that GPT was associated with the GMVs in the right lateral frontal pole cortex, left ventromedial prefrontal cortex, right lateral occipital cortex, and right occipital pole. Additionally, we observed that the amount-relevant brain activations (responding to reward circuitry) in the lateral orbitofrontal cortex were negatively associated with individual’s variability in GPT scores, whereas the delay time-relevant brain activations (responding to prospection network system) in the dorsolateral prefrontal cortex, dorsomedial prefrontal cortex, superior parietal lobule, and anterior cingulate cortex were positively associated with individual’s variability in GPT scores. These findings not only provide novel insights into the neuroanatomical substrates underlying the human dispositional greed, but also suggest the critical roles of reward and prospection processing on the greed.

Keywords
Greed · Multivariate pattern analysis · VBM · Reward circuitry · Intertemporal choice

Introduction
Financial problems, while often relegated to individual concern, may manifest as large-scale crises when left to further develop adversely. The traditional viewpoint proposes that the causes for these crises largely lay in structural problems, such as the rise of national debts or failures in financial regulation. Contemporary theories highlight some underlying psychological components, such as greed personality trait (GPT), that likewise play a critical role in financial behaviors (Seuntjens et al. 2016). For instance, individuals with more available income were found to exhibit greater dispositional greed which, in turn, was associated with problematic financial outcomes, such as less saving and greater monthly spending and likelihood of accruing debt (Seuntjens et al. 2016). To date, greed has been discussed in a variety of fields, including economic psychology (Wang and Murnighan 2011), marketing (Krekels and Pandeelaere 2015), religion studies (Aimran et al. 2014), and neuroscience (Li et al. 2019; Mussel et al. 2015). Intuitively, greed is frequently characterized as being closely correlated with money and economic values, such as wealth, materialism, self-interest, and power-striving (Rokeach 1973; Tang 2007; Schwartz 1992). Outside the realm of monetary transactions, greed has also been associated with antisocial, unethical, and
deviant behavior (Krueger et al. 2007; Patrick et al. 2005). Although the general connotations surrounding greed lean toward the negative, however, it has nonetheless been shown to yield some positive outcomes on societal and economic systems (Domínguez 2014; Bruhn and Lowrey 2012), such as in motivating people to complete goals and strive for greater performance in pursuit of a better life (Levine 2000). The double-edged nature of greed has notably been gaining increased attention among scholars in the scientific community.

In the past decade, a pervasive and critical issue in the domain of greed study has been how to quantitatively measure and scientifically define greed. This issue has presumably been one of the main reasons for the limited number of empirical studies in investigating greed. Presumably inspired by the financial crises of late, several relevant measures of greed have been developed in the past decade, including the Virtues and Vices Scale (VAVS) (Veselka et al. 2014), the Greed Trait Measure (Mussel et al. 2015), the GR€€D scale (Mussel and Hewig 2016), the Dispositional Greed Scale (DGS) (Krekels and Pandelaere 2015), and another DGS developed by Seuntjens, Zeelenberg, van de Ven, and Breugelmans (2015). Such measures have provided a novel window into investigating the psychological construct of greed. A recent prototype analysis suggested two parallel aspects of GPT, including the “experience of desiring to acquire more and the dissatisfaction of never having enough” (Seuntjens et al. 2015, p. 518). When defined as such, greed may be conceived as the possible result of both striving toward the positive outcome of obtaining desired benefits as well as withdrawing from the negative state of not having these benefits. Thus, greed might largely be associated with a specific reward system that directly determines the motivation to withdraw and approach. However, greed as a personality trait is nuanced and multidimensional in nature (Krekels and Pandelaere 2015; Mussel et al. 2018), which calls for more empirical investigation in tandem with behavioral estimation, computational models, and brain function imaging, in addition to advanced statistical models and techniques.

Although the history of research in greed is long-standing, the field has observed a scarcity of greed studies in the field of neuroscience. An early Electroencephalography (EEG) study on greed reported that greedy individuals exhibited a reduced feedback-related negativity difference to unfavorable outcomes relative to favorable outcomes in risky decision-making (Mussel et al. 2015). Another recent EEG study observed a reduced P300 effect to positive feedback compared to negative feedback in individuals with high trait greed (Mussel and Hewig 2019). Both studies emphasized disrupted learning capacity from experiences and environment for greedy individuals. In contrast, the first functional magnetic resonance imaging (fMRI) study revealed a mediation effect of the neural responses in the ventromedial prefrontal cortex/medial orbitofrontal cortex (VMPFC/mOFC) between individual differences in GPT scores and behavioral loss aversion (Li et al. 2019). This study hints that the functional characteristics of VMPFC/mOFC are critical for understanding the neural substrates of GPT, especially for understanding their decision features. However, whether the morphological characteristics of VMPFC/mOFC are associated with greed personality trait remains elucidated.

It has been proposed that greedy individuals exhibit behavioral impulsivity stemming from more short-sighted, rather than far-sighted, thinking (Li et al. 2019). The notion that greed and impulsivity go hand in hand does not merely remain theoretical. Indeed, evidence from behavioral studies partially supports the view that far-sighted thinking could predominantly reduce greediness (Sjåstad 2019). In a laboratory setting, one of the most effective paradigms to assess individual’s short- and far-sighted thinking is the inter-temporal choice task, in which subjects are required to gauge and weigh the tradeoff between the cost of time and associated benefits (Bickel et al. 1999). Functional imaging studies have suggested that there is a valuation network that preferentially processes the attribution of the magnitude of future benefits, consisting of several brain regions, such as the VMPFC, mOFC, posterior cingulate cortex (PCC), and ventral striatum (VS) (Ballard and Knutson 2009; Li et al. 2013; Kable and Glimcher 2007; Wang et al. 2014). In addition, the prefrontal-parietal network, including the dorsolateral prefrontal cortex (DLPFC) and superior parietal lobule (SPL), was thought to represent the delay time length of future alternatives (Ballard and Knutson 2009; Li et al. 2013). Both brain activations in these two networks were significantly associated with individuals’ short-sighted behaviors (Ballard and Knutson 2009). Yet, whether brain activations can predict GPT remains unanswered.

To date, the multivariate pattern analysis (MVPA) approach has been widely utilized to investigate the neural mechanisms of higher cognitive processes and personality, providing a novel tool to capture the principles of how the human brain functions (Haxby et al. 2014; Ritchie et al. 2019; Henningsgaard and Arnau 2008; Nostro et al. 2018). Compared to the traditional univariate approach, MVPA has many advantages, including greater sensitivity in the detection of cognitive states, capturing the structure of the neural coding in the brain, and bridging the brain functional/structural index and behavioral performances (Norman et al. 2006; Haxby 2012; Wang et al. 2014, 2016). Lending to the aforementioned merits, we sought to uncover the novel story for the neural bases in GPT using the univariate and multivariate analysis approach. We hypothesized that the GMV in VMPFC/mOFC would be significantly correlated with individual’s variability in GPT via univariate analysis and could successfully predict an individual’s GPT via MVPA.
Additionally, regarding the close association between greed and far-sighted thinking, we hypothesized that the brain activations in response to the magnitude and time of future rewards could predict individual variation in GPT.

**Materials and methods**

**Subjects**

Sixty-two subjects (26 males; age ranged from 18 to 26 years old; Mean age ± SD = 20.98 ± 1.43) participated in our study and their structural MRI data were collected. Twenty-four subjects (8 males; age ranged from 19 to 24 years old; Mean age ± SD = 21.21 ± 1.22) performed an inter-temporal choice task while their functional MRI data (fMRI) were collected. Five volunteers of this fMRI experiment task were subsequently excluded from the following analyses due to either large head motion (three subjects, mean framewise displacement [FD] > 0.5 mm in any one of three runs) or misunderstanding the task instructions (two subjects). Hence, this study included 62 structural MRI data and 19 functional MRI data. All subjects were free from neurological or psychiatric history. Informed written consent was obtained from subjects before formal experiments were conducted. This study was approved by the Institutional Review Board of the Faculty of Psychology at Tianjin Normal University (No. XL2020-27), China.

**Assessment of greed personality trait**

GPT was measured via a 7-item Dispositional Greed Scale (DGS) (Mussel et al. 2018; Seuntjens et al. 2015), that has been evidenced to yield high reliability and validity. Subjects indicated the extent to which they agreed with each item presented in the scale (e.g., “One can never have too much money”). All items were rated on a 5-point Likert-scale (1 = ‘strongly disagree’ to 5 = ‘strongly agree’). The total scores range from 7 to 35, whereby higher scores indicated higher levels of greedy personality.

**Intertemporal choice task**

Figure 1 depicts the stimuli and the experimental procedures of the inter-temporal choice task. Subjects were instructed to choose between a fixed immediate reward (RMB 40—approximately USD 6) and a delayed reward that varied across trials. To estimate the neural responses to the amount and delay time of future rewards, the two dimensions were manipulated independently and orthogonally, with the amount ranging from RMB 40 to 115 (16 levels in increments of RMB 5), and the delay ranging from 1 to 150 days (16 levels in 9- or 10-day increments). These ranges were chosen based on previous studies (Wang et al. 2014) and an additional pilot study of an independent sample (n = 12). All possible combinations of each amount and delay level yielded a total of 256 trials, which were pseudo-randomly

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![Fig. 1](image.png)

An illustration of the event-related experimental design. During each trial, the amount and delay time of a future reward were presented side by side divided by a vertical line on the screen (for 3 s), but the immediate option (RMB 40) was told to the participants but not displayed visually. Participants were required to decide between the immediate and delayed alternatives based on their preference. The chosen option turned yellow after participants made their choice. The amount and time of delayed rewards for each trial were sampled from the amount/time matrix, shown here as one sample trial. A decision from each cell in this 16 × 16 matrix was presented during scanning, but the data were collapsed into a 4 × 4 matrix for analysis. The inter-stimulus interval (ISI) was jittered to optimize design efficiency.
divided into three runs. We utilized an event-related fMRI design and optimized the timing and order of stimulus presentation using optseq2 to maximize the estimation efficiency (Dale 1999).

Following a similar procedure done in a previous study (Wang et al. 2014), for each trial, the amount and delay time of the future reward were shown on the screen but the fixed, immediate reward was told to the participant beforehand and not shown. The amount and the delay time appeared side by side divided by a vertical line (see Fig. 1) and whether the amount or the delay time appeared on the right side was determined randomly. Subjects were asked to respond as quickly as possible within the designated 3-s trial duration. If no response was made within this window, the task continued to the next trial. The trials with no responses were modeled as a separate regressor of no interest in the general linear model (GLM). To best capture subjects’ true preference for each decision, compared to a fixed, dichotomous decision rule (Tom et al. 2007), subjects indicated one of four possible responses to each decision (e.g., “strongly choose the immediate option”, “moderately choose the immediate option”, “moderately choose the delayed option”, “strongly choose the delayed option”) using a four-button response box. After each decision, the chosen option turned yellow as a feedback indication.

At the end of the experiment, all participants received the non-contingent compensation of RMB 50 plus a bonus based on the amount they actually earned on one randomly chosen trial (i.e., the participants did not receive the actual total amount earned). In other words, each participant received RMB 50 + either 40 (for choosing the immediate reward, with the total amount paid at the end of the experiment) or 45–115 (for choosing the delayed reward, with non-contingent compensation paid at the end of the experiment and the bonus paid as dictated by the delay time).

**Brain imaging data acquisition**

Whole-brain image 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. Subjects laid supine on the scanner bed and viewed visual stimuli back-projected onto a screen through a mirror attached to the head coil in a decision task. Foam pads were utilized to minimize head motion. High-resolution T1-weighted structural images were acquired using MP-RAGE sequence and the following parameters were used: repetition time (TR) = 2530 ms; echo time (TE) = 2.98 ms; multi-band factor = 2; flip angle = 7°; field-of-view (FOV) = 224 × 256 mm²; slices = 192; voxel size = 0.5 × 0.5 × 1 mm³. The T2*-weighted functional images used the following parameters: TR = 2000 ms; TE = 30 ms; multi-band factor = 2; flip angle = 90°; FOV = 224 × 224 mm²; slice thickness = 2 mm; slice gap = 0.3 mm; voxel size = 2 × 2 × 2 mm³. The slices were tilted ~ 30 degrees clockwise from the AC-PC plane to obtain better signals in the orbitofrontal cortex.

**Structural MRI preprocessing and statistical analysis**

Structural MRI data were collected using the Oxford Centre for Functional MRI of the Brain (FMRI) Software Library voxel-based morphometry (FSL-VBM), a VBM style analysis toolbox implemented in FSL (version 6.00; part of the FSL package: http://www.fmrib.ox.ac.uk/fsl). Brains from the structural images were extracted, tissue-type segmented, and then aligned to the gray matter template in the MNI152 standard space. The spatially normalized images were then averaged to create a study-specific template, to which the native gray matter images were registered again using linear and nonlinear algorithms. The registered partial volume images were then modulated by dividing them with the Jacobian of the warp field to correct for local expansion or contraction. The modulated segmented images, which represented the GMV, were then smoothed with an isotropic Gaussian kernel with 3 mm standard deviation. The smoothed data were used for the univariate analysis. In addition, we used unsmoothed GMV for further MVPA.

First, we examined associations between GPT and GMV in whole-brain level using a mixed-effects FLAME 1 model implemented in FSL. Maternal education, paternal education, age at MRI scan, and total GMV were included as covariates. These factors were taken into account because behavioral correlation analysis revealed that maternal and paternal education might account for relatively large variations of GPT, although their correlations were not significant. In regression analysis, covariates were entered into the first block of equations. In the second block, mean-centered GPT and gender were entered. The interaction term, the product of mean-centered GPT and gender were entered into the third block. When the interactive effect was not significant, a reduced model, controlling for the same covariates and gender, examined GPT in relation to the same outcome measures. Statistical results were determined at a cluster level (z > 2.3, p < 0.01) and at a family-wise error rate of 0.05 for the correction for multiple comparisons using Gaussian Random Field Theory.

Second, in the multivariate pattern analysis, Epsilon-insensitive support vector regression (SVR) (Drucker et al. 1997) with a linear kernel, as implemented in PyMVPA (http://www.pymvpa.org) (Hanke et al. 2009), was used to examine the associations between the GPT and GMV in whole-brain level. A searchlight procedure with a three-voxel radius (Kriegeskorte et al. 2006) was employed to provide a measure of decoding accuracy in the neighborhood of each voxel. Given previous studies (Wang et al. 2014; Jimura and Polidrak 2012), we set the ε parameter...
in the SVR to be 0.01. A three-fold cross-validation was applied in this study. The 62 subjects were divided into three groups of 20 or 21 subjects, with matched gender as well as matched GPT. In each iteration, an SVR model was trained based on two groups of 41 or 42 subjects. Once trained, this SVR model then was applied to test the generalization on the remaining one group based on their imaging data. It is worth noting that the training dataset was first normalized (i.e., mean subtracted out and then divided by SD) and then applied to testing dataset. The voxel-wise accuracy of SVR prediction was then calculated as the Pearson’s correlation coefficient between actual and predicted values of the GPT and then transformed to the corresponding z-score maps. Finally, SVR predictions were thresholded using cluster detection statistics, with a height threshold of \( z > 2.3 \), and a cluster probability of \( p < 0.05 \), corrected for whole-brain multiple comparisons using Gaussian Random Field Theory.

To further probe the direction of the associations between GMV and GPT, we selected the clusters showing significant prediction accuracy of GPT as ROIs. The averaged GMV was then extracted and performed a Pearson’s correlational analysis between ROI’s GMVs and GPT. To avoid the double dipping issue, we only reported the positive and negative analysis between ROI’s GMVs and GPT. The averaged GMV and GPT, we selected the clusters showing significant prediction in MVPA, respectively, from the univariate and multivariate analyses to directly compare the effect of univariate and multivariate statistics via Pearson’s correlational analysis.

**Functional MRI preprocessing and statistical analysis**

The FMRI Expert Analysis Tool was used to perform the functional image preprocessing and statistical analyses. The scanner allowed discarding the first four volumes for T1 equilibrium before the task. The remaining images were then realigned to correct for head movements. Data were spatially smoothed using a 5 mm full width at half maximum Gaussian kernel and filtered in the temporal domain using a nonlinear high-pass filter with a 90 s cutoff. EPI images were first registered to the MPRAGE structural images and then into MNI standard space, using affine transformations (Jenkinson and Smith 2001). Registration from MPRAGE structural images to standard space was further refined using FNIRT nonlinear registration (Anderson et al. 2007). Statistical analyses were first performed in the native image space, with the statistical maps normalized to the standard space before higher-level analysis.

The data were modeled at the first level using a general linear model within FSL’s FILM module. Five parametric regressors were included during the decision-making period starting from presentation of inter-temporal alternatives and ending when subjects responded: (1) the overall task regressor (1 for each trial); (2) the amount of delayed reward; (3) the time of delayed reward; (4) the relative value, calculated using the following formula: relative value = abs(immediate–delayed amount \( \times k \) ) (FitzGerald et al. 2009; Lim et al. 2011); (5) reaction time (RT) (Sripada et al. 2011). For this model, each regressor (except for the task regressor) was first demeaned and normalized to the same range (−1 vs 1) and then convolved with the double-gamma canonical hemodynamic response function. Trials with no valid response were modeled as a separate regressor of no interest.

A second-level analysis was performed using a fixed-effect model where all three functional runs were combined within individual participants. Finally, these contrast results were then fed into a random-effect model for group analysis and regression analysis for each individual’s GPT scores using a FLAME1 model. Group images were thresholded using cluster detection statistics, with a height threshold of \( z > 2.3 \) and a cluster probability of \( p < 0.05 \), corrected for whole-brain multiple comparisons using Gaussian Random Field Theory.

**Results**

**Demographics**

In the structural dataset, the GPT scores ranged from 13 to 35 (Mean ± SD = 20.98 ± 1.43). Gender differences were not observed in the GPT scores \( (t_{(60)} = 1.060, p = 0.294, d = 0.273) \). The GPT scores did not vary significantly by age \( (r_{(60)} = −0.073, p = 0.573) \), paternal education level \( (r_{(60)} = 0.103, p = 0.427) \), or maternal education level \( (r_{(60)} = 0.133, p = 0.303) \). In the functional dataset, the mean ± SD of GPT scores and delay discounting rates (k) were 21.33 ± 4.74 and 0.015 ± 0.017, respectively. Similarly, GPT scores were not correlated with age \( (r_{(17)} = −0.031, p = 0.904) \), paternal education level \( (r_{(17)} = 0.240, p = 0.337) \), or maternal education level \( (r_{(17)} = 0.213, p = 0.396) \). Furthermore, GPT scores did not vary significantly as a function of k \( (r_{(17)} = −0.080, p = 0.753) \), which suggested that individuals with high greed scores did not exhibit impulsive behavior.

**VBM results**

The present study aimed to explore the structural substrates of GPT. First, traditional univariate analysis was used to examine whether there was an interaction effect between gender and GPT in GMV due to males more frequently exhibiting greedy behaviors than females (Krekels and
Pandelaere 2015). However, the interaction between gender and GPT did not predict grey matter volume at the whole-brain analysis. The reduced model also did not observe a main effect of GPT in the grey matter volume even after controlling for age, gender, paternal and maternal education, and total GMV.

MVPA has been demonstrated to be more sensitive to distributed coding of information and detecting brain-behavior associations than univariate analysis (Jimura and Poldrack 2012). Therefore, this approach was used to examine the associations between GPT and brain morphological index. As expected, MVPA revealed that GPT was associated with the GMVs in the right lateral frontal pole cortex (LFPC; peak MNI = −16, 60, 16, Z = 3.38; cluster size = 474) (Fig. 2a), left ventromedial prefrontal cortex (vmPFC; peak MNI = −14, 58, 14, Z = 3.51; cluster size = 687) (Fig. 2b), right lateral occipital cortex (LOC; MNI = 34, −82, 34, Z = 3.51; cluster size = 644) (Fig. 2c), and right occipital pole (OP; MNI = 10, −102, −2, Z = 3.59; cluster size = 697) (Fig. 2d). In probing the direction of the associations between these ROIs’ GMVs and GPT, a further correlational analysis indicated that GPT was negatively associated with the GMVs in the LFPC, vmPFC, LOC, and OP (Fig. 2e–h).

To directly compare the univariate and MVPA results, $z$ statistics of each voxel in the ROIs’ area were plotted. As shown in the Fig. 2i–l, there were significant correlations between the $z$ statistics of the two analyses in the LFPC ($r(60) = -0.970$, $p < 0.001$), vmPFC ($r(60) = -0.468$, $p < 0.001$), LOC ($r(60) = 0.520$, $p < 0.001$), and OP ($r(60) = 0.618$, $p < 0.001$), and obviously distributed on the upper diagonal line (i.e., larger $z$ statistics), which suggested that the effect size was lower for univariate analysis compared to MVPA.

**fMRI results**

Here, we further examined whether the brain activations related to future-oriented rewards were associated with individuals’ variability in GPT. As expected, the whole-brain analysis revealed that brain activations responding to direct comparison.
to the magnitude of future rewards were significantly and negatively correlated with the GPT in the left lateral OFC (LOFC; Peak MNI = −38, 24, −12, Z = 3.71) (Fig. 3a, c). Similar patterns were found in the left LOC (MNI = −18, −68, 58, Z = 3.86), left inferior temporal gyrius (ITG; MNI = −58, −62, −6, Z = 3.90), right superior parietal lobule (SPL; MNI = 20, −46, 62, Z = 4.32), and right postcentral gyrus (MNI = 16, −46, 62, Z = 4.11) (Fig. 3a). Table 1 provides the specific information, including cluster size. Taken together, reward-amount-related brain activations could predict individual variability in GPT.

Whether the brain activations in response to the delay time of future rewards were correlated to GPT were further examined. Interestingly, the whole-brain analysis likewise indicated that brain activations responding to the time attribution of future rewards were positively correlated with the GPT in the right lateral frontal pole cortex (LFPC, MNI = 22, 48, 22, Z = 5.14) (Fig. 3b, f), left dorsolateral prefrontal cortex (DLPFC, MNI = −30, 6, 68, Z = 3.96) (Fig. 3b, d), left dorsomedial prefrontal cortex (DMPFC, MNI = −14, 4, 58, Z = 3.83) (Fig. 3b, h), right anterior cingulate cortex (ACC, MNI = 6, 34, 26, Z = 3.43) (Fig. 3b, g), left superior parietal lobule (SPL, MNI = −26, −46, 34,

Fig. 3  Brain region activations responding to the amount and delay time of future rewards associated with GPT. Neural responses to the amount of future rewards were negatively correlated with the GPT (a) whereas the delay time-related neural responses were positively correlated with the GPT (b). Percentage signal change was also linearly associated with GPT in LOFC (c), DLPFC (d), SPL (e), LFPC (f), ACC (g), and DMPFC (h). These ROIs were selectively presented based on their importance on the processing of reward amount and delay time. LOFC lateral orbitofrontal cortex, DLPFC dorsolateral prefrontal cortex, SPL superior parietal lobule, LFPC lateral frontal pole cortex, ACC anterior cingulate cortex, DMPFC dorsomedial prefrontal cortex.
Z = 3.41) (Fig. 3b, e). Similar patterns were also observed in the right precentral gyrus (MNI = 50, 2, 56, Z = 3.42), and left precuneus (MNI = −12, −46, 44, Z = 3.30). Table 1 provides the specific information, including cluster size. Taken together, delay time-related brain activation could also predict individual differences in GPT.

Discussion

The present study examined the neural substrates of GPT via univariate and multivariate analysis approaches. At the structural level, MVPA results revealed that the GMVs in the prefrontal and visual system were associated with individual variability in GPT. At the functional level, brain activations responding to the two components of future rewards (i.e., amount and delay time) were both associated with GPT. To the best of our knowledge, this is the first work to symmetrically investigate the structural and functional substrates of greed and consistently highlight the importance of prefrontal cortices in GPT.

Our multivariate analysis revealed that greedier individuals exhibited smaller GMV in the LFPC and VMPFC. The LFPC and VMPFC are, respectively, distributed in the lateral and medial part of frontal pole cortex that has unique cytoarchitectonic characteristics relative to the rest of the prefrontal cortex (Öngür et al. 2003). With regard to the posterior–anterior hierarchy of the prefrontal cortex, LFPC located at the top position is thought to engage in a set of more abstract mental processes, such as executive control (Badre and Nee 2018), mentalizing (Gallagher and Frith 2003), thinking of the future (Okuda et al. 2003; Peters and Büchel 2010a), and exploratory decision (Daw et al. 2006; Badre et al. 2012). Neuroanatomical studies have also indicated that GMV in the LFPC and its functional connections with VMPFC and VS were correlated with individuals’ short-sight behaviors (Wang et al. 2016, 2020a). Additionally, the LFPC is able to modulate the hippocampal functional activity to strengthen people’s ability in episodic future thinking (Schachar et al. 2007; Lebreton et al. 2013). Furthermore, prior studies have also demonstrated that LFPC represents the subjective value of future options (Wang et al. 2014). Nevertheless, functional activation results in this study showed that activity in LFPC, which represents the delay time of future rewards, was positively correlated with GPT, suggesting that greedy people perhaps display altered future time perception.

VMPFC is a core sub-region of the reward circuitry (Haber and Knutson 2010) and represents primary and secondary rewards with a way of neural common currency (Levy and Glimcher 2012; Saxe and Haushofer 2008). This region tracks the subjective value of various types of environmental stimuli across a myriad of different properties, such as risk (Xue et al. 2009), probability (Seaman et al. 2018), time (Kable and Glimcher 2007), and effort (Seaman et al. 2018). Considerable studies have indicated that brain activity in this region directly correlates with rating of pleasantness (Peters and Büchel 2010b; Kühn and Gallinat 2012). Patients with VMPFC-lesion exhibited large changes in personality characterized by shallow affect, callous lack of empathy, impulsivity, and irresponsibility (Schneider and Koenigs 2017). Numerous theories focusing on the VMPFC function have also emphasized a critical role of this region on the generation and regulation of emotion (Damasio 1996; Bechara and Damasio 2005). Based on these findings, people with high GPT scores might exhibit aberrant morphological

| Effect  | Brain Region      | Cluster size (voxels) | MNI Coordinates | Z  |
|---------|------------------|-----------------------|-----------------|----|
| Amount  | L LOFC           | 268                   | −38 24 −12      | 3.71|
|         | R SPL            | 217                   | 20 −46 62       | 4.32|
|         | R postcentral    | 248                   | 16 −46 62       | 4.11|
|         | L LOC            | 268                   | −18 −68 58      | 3.86|
|         | L inferior temporal gyrus | 294 | −58 −62 −6 | 3.90|
| Time    | R LFPC           | 854                   | 22 48 22        | 5.14|
|         | L DLPFC          | 218                   | −30 6 68        | 3.96|
|         | L DMPFC          | 52                    | −14 4 58        | 3.83|
|         | R ACC            | 128                   | 6 34 26         | 3.43|
|         | L SPL            | 192                   | −26 −46 34      | 3.41|
|         | R precentral     | 132                   | 50 2 56         | 3.42|
|         | L precuneus      | 54                    | −12 −46 44      | 3.30|

LOFC lateral orbitofrontal cortex, SPL superior parietal lobe, LOC lateral occipital cortex, LFPC lateral frontal pole cortex, DLPFC dorsolateral prefrontal cortex, DMPFC dorsomedial prefrontal cortex, ACC anterior cingulate cortex, L left, R right
characteristics in reward system and affect network, which is more consistent with the definition of greed as the experience of desiring more and the dissatisfaction of never having enough.

Beyond the prefrontal system, the visual system, such as the LOC and OP, was also found to be associated with GPT in the current study. The activation of the visual system has often been detected in various cognitive tasks studies and was thought to predominantly involve stimulus salience processing and attention distribution (Grill-Spector and Malach 2004). This system develops very early and is more vulnerable to adverse childhood experiences, such as postnatal maternal depression (Shaw et al. 2008; Teicher et al. 2016; Wang et al. 2019a). Aberrant development of the visual system not only impacts the information processing of external world, but also reshapes the structural and functional links with higher cortical areas, sub-serving various cognitive processes like reward processing (Wang et al. 2019b, 2020b). Additionally, previous neuroanatomical studies also reported the associations between five-factor model of personality and morphological index (i.e., cortical volume, thickness, and surface area) in the visual system (Riccelli et al. 2017). Hence, individuals with higher GPT scores may exhibit varied spatial information processing to external environmental cues, especially to threatening stimuli, which may further give rise to greedy, risky, and impulsive behaviors.

At the functional level, we found that lateral OFC activation responding to reward amount of future benefits was negatively correlated with GPT. Converging evidences from human functional imaging studies have shown that lateral OFC is more involved in representing negative reinforcers, resulting in increased activity as negative rewards also increase (Peters and Büchel 2010b). Meta-analysis studies likewise support the view that lateral OFC is related to monetary loss (O’doherty et al. 2001; Kringelbach and Rolls 2004). Additionally, a number of impulsive behaviors were characterized by hyperactivation in the reward/approach system in contrast to hypoactivation in the punishment/avoidance system (Gable 2006). Such approach-avoidance motivation hypothesis is frequently used to describe personality like extraversion and neuroticism (Elliott and Thrash 2002). Intuitively, greedy traders are often associated with self-interest and maximization, both of which might depend on the function of the lateral OFC, without considering the loss, cost, and risk (Constantinople et al. 2019). Additionally, lateral OFC activation responding to reaction time was also positively correlated with GPT (see Supplementary Material for details), which might further hint that value-based decisions possibly enhance the decision difficulty and conflicting between different alternatives for greedier individuals.

Beyond the reward system, we identified the time-related processing system of prefrontal and parietal cortices that also exhibited special activation features in greedy individuals. The prefronto-parietal cortices are predominantly comprised of a lot of brain areas, including the DLPFC, ACC, SPL, and DMPFC in present study, and are frequently thought to play critical roles in various cognitive processes, such as goal maintenance, information updating, working memory, and executive control (Blumenfeld and Ranganath 2007; Lara and Wallis 2015; van Noordt and Segalowitz 2012; Tanji and Hoshi 2001). In the decision-making domain, the prefronto-parietal network is able to down-modulate valuation and reward processing (Peters and Büchel 2011; Hare et al. 2009; Wang et al. 2020c) and determine the exploration–exploitation decisions (Laureiro-Martinez et al. 2015). In addition, considerable studies have implicated the prefronto-parietal cortices in the time perception that further contributes the decision-making, such as short-sighted choices (Wittmann and Paulus 2008; Harrington et al. 1998).

There are several limitations to consider in this study. First, the sample size in the current functional dataset is relatively small and might limit the generalizability of our conclusion to a larger population. Recently, a number of studies have systematically investigated the consequences of sample size on stability and interpretation of brain-behavior correlations in task-based and resting-state-based fMRI data (Grady et al. 2021; Braver et al. 2010; Dubois and Adolphs 2016). As small sample sizes can increase sampling and false-positive error, sex differences and functional findings in the current study should be interpreted with caution. Secondly, although maternal and paternal education levels have been controlled for as possible confounding covariates in our statistical models, the subjects’ own education attainment may still play a role in greed personality trait. Subject education attainment was not included or measured in the current study and future examination may be warranted. Lastly, the examined sample ranged from ages 18–26, limiting the generalizability of findings to a wider age bracket. Further research is necessary to examine the effects of brain development and behavioral variations on greed personality.

In conclusion, the present study examined the neural substrates of GPT using both the univariate and multivariate pattern approach. Our findings revealed the importance of morphological and functional architecture of prefronto-parietal and visual cortices in their relation to GPT. These findings provide novel insights into the cognitive and neural mechanisms of greed, especially from the perspective of the reward- and time-related functional networks.

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Data availability statement  The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest  The authors declare that they have no conflict of interest.

Ethical 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.

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