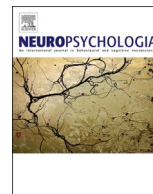




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Sex difference in neural substrates underlying the association between trait self-control and overeating in the COVID-19 pandemic

Qingqing Li, Guangcan Xiang, Shiqing Song, Yuhua Li, Xiaoli Du, Xinyuan Liu, Hong Chen^{*}

Key Laboratory of Cognition and Personality, Ministry of Education, Faculty of Psychology, Southwest University, Chongqing, 400715, China

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ABSTRACT

During the COVID-19 pandemic, people are at risk of developing disordered eating behaviors. The present study utilized resting-state functional magnetic resonance imaging (fMRI) to examine how trait self-control and its neural mechanisms predict overeating tendencies in young adults during the pandemic. Data on trait self-control, the amplitude of low-frequency fluctuation (ALFF), and resting-state functional connectivity (RSFC) were collected before COVID-19 (September 2019, T1), and data on overeating were collected during COVID-19 (February 2020, T2). Whole-brain regression analyses ($N = 538$) revealed that higher trait self-control was associated with higher ALFF in the right dorsolateral and ventrolateral prefrontal cortex (DLPFC, VLPFC) and the left anterior insula, and lower ALFF in the left fusiform gyrus and precuneus. With the DLPFC, fusiform gyrus and precuneus as seed regions, trait self-control was associated with decreased connectivity of the orbitofrontal cortex, anterior cingulate cortex, temporal pole, and insula, and increased connectivity between the right VLPFC and anterior cerebellum. Longitudinal mediation models showed that trait self-control (T1) negatively predicted overeating (T2), and the mediating effects of the fusiform gyrus, DLPFC, and VLPFC were moderated by sex. The present study reveals that the brain networks for trait self-control are mainly involved in cognitive and executive control and incentive and emotional processing, demonstrating the longitudinal benefits of trait self-control in alleviating disordered eating behaviors during the pandemic. Sex differences in the neural substrates underlie this association. These findings may have implications of the interventions for behavioral maladjustment.

1. Introduction

As coronavirus disease 2019 (COVID-19) has quickly spread globally, it has negatively impacted people's physical and mental health. This includes disordered eating behaviors, which researchers have demonstrated some people are at increased risk of developing during the COVID-19 pandemic (Rodgers et al., 2020). Overeating, a typical form of disordered eating, refers to uncontrolled eating behavior in which individuals eat more food than they need for energy (Prentice, 2001). Studies have shown that sustained overconsumption of food is closely related to physical (e.g., obesity) and psychological problems (e.g., body dissatisfaction) (Goossens et al., 2009). In the field of health psychology, self-control is defined as the ability to regulate unhealthy desires or impulses in order to meet more valued goals (De Ridder et al., 2012; Tangney et al., 2004). Existing evidence from different populations has shown that self-control is regarded as a great human strength and is associated with many positive outcomes, such as improved academic

and work performance, personal adjustment, interpersonal functioning, fitness, and well-being (Allemand et al., 2019; De Ridder et al., 2012). (see Table 3)

The benefits of self-control on healthy eating behaviors are also well documented. Specifically, individuals with high self-control capacity generally have healthy dietary beliefs and eating habits, and are less likely to exhibit disordered eating behaviors or regularly consume unhealthy foods (Gillebaart et al., 2016; Junger and Van Kampen, 2010). Individuals with low levels of self-control ability, however, tend to engage in overeating (Meule and Platte, 2015) and make unhealthy dietary choices, such as consuming excessive amounts of high-calorie foods and snacks (Nederkoorn et al., 2010) and have a generally higher saturated fat intake (Allom and Mullan, 2014). Furthermore, longitudinal studies indicate that individuals with high self-control ability are more likely to lose more weight and avoid the risk of overweight, compared to the low counterparts (Tsukayama et al., 2010). Therefore, in the present study, it is assumed that trait self-control could

^{*} Corresponding author. Faculty of Psychology, Southwest University, Tiansheng Road No.2, Beibei District, Chongqing, China.

E-mail addresses: 463850987@qq.com (Q. Li), 741880270@qq.com (G. Xiang), song_19921014@163.com (S. Song), liyuhua0321@163.com (Y. Li), 1406616719@qq.com (X. Du), 499701396@qq.com (X. Liu), chenhswu@163.com (H. Chen).

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be negatively associated with overeating during the COVID-19 pandemic.

According to the dual-system model, the success or failure of employing self-control in eating decisions reflects the competition between the cognitive control/reflective system and socioemotional/affective system (Steinberg, 2010). The socioemotional system, characterized by affective and impulsive processes, can be easily triggered by impulses and immediate rewards. The cognitive control system, characterized by reflective and deliberate processes, can regulate automatic impulses and facilitate long-term goals. Neuroscience studies indicate that the reflective and socioemotional systems are distributed in the cortical and subcortical brain regions (Steinberg, 2010). Functional and structural neuroimaging studies have consistently shown that the dorsolateral prefrontal cortex (DLPFC) and ventrolateral prefrontal cortex (VLPFC), the most notable brain areas in the reflective system, are closely linked to deliberative processing, motor inhibition, executive control, and affective regulation (Aron et al., 2014; Levy and Wagner, 2011; McClure and Bickel, 2014). Lopez et al. (2014) reported that individuals with higher VLPFC activation in an inhibition task were more likely to consume less unhealthy food. Furthermore, Hare et al. (2009) found an accompanying activation in the DLPFC when individuals made healthy choices in accordance with their dietary goals, while activity in this brain region was reduced when participants made impulsive choices. Studies of intertemporal decisions have also shown that selecting delayed rather than immediate rewards is associated with increased DLPFC activity (McClure et al., 2004). Thus, the function of the lateral prefrontal cortex (DLPFC, VLPFC) may be closely related to self-control capacity and overeating.

Self-control ability is not only dependent on cognitive and executive control function in the reflective system but also related to incentive and emotional processing in the affective system (Heatherton and Wagner, 2011). Behavioral findings suggest that the enactment of self-control do not necessarily need to be the result of effortful inhibition of undesirable responses (De Ridder and Gillebaart, 2017). Individuals with high trait self-control are inclined to maintain healthy habits (Galla and Duckworth, 2015) and report fewer problematic desires and conflict when facing temptation (Hofmann et al., 2012). Conversely, individuals with insufficient self-control resources tend to show higher emotional reactivity and have difficulties in resisting tempting stimuli (Wagner and Heatherton, 2013). This suggests that people with high self-control ability may be less influenced by automatic impulses and emotional interference. Neuroimaging studies show that groups with inadequate self-control capacity (e.g., obesity, restrained eating) show stronger activation in brain areas involved in desire, incentive value, and emotional processing, including the orbitofrontal cortex (OFC), striatum, and insula, as well as the fusiform gyrus and precuneus during presentation of appetitive cues (e.g., palatable and high-calorie foods) (Burger and Stice, 2011; Coletta et al., 2009; Uher et al., 2006). Furthermore, the increased activation in incentive and emotional processing regions and decreased activation in cognitive control regions were associated with future weight gain and overeating (Willeumier et al., 2011; Yokum et al., 2011). In addition to activity in brain regions, connectivity strength between different brain regions can also reflect individuals' self-control ability and account for the association of their self-control ability with eating decisions. For instance, the prefrontal cortex exerts top-down control to lead to goal-directed behavior and inhibit inappropriate response tendencies through the fronto-subcortical circuits (Miller and Desposito, 2005).

Existing studies have mostly used task-related fMRI designs to investigate the neurobiological substrates of individual self-control ability; thus, little is known about spontaneous brain activity associated with trait self-control during a resting state. It should be noted that stable individual personality differences are more clearly manifested in overall brain structure and function, and task-free rather than task-specific designs may be advantageous for examining the neural substrates underlying self-control ability. Resting-state functional magnetic

resonance imaging (rsfMRI) is a reliable and frequently used task-free method of examining intrinsic brain activity and connectivity (Zuo and Xing, 2014). Two reliable and sensitive measures are commonly used: amplitude of low-frequency fluctuations (ALFF), reflecting the regional properties of spontaneous neural activity at rest, and resting-state functional connectivity (RSFC), reflecting the synchronization and functional connections between brain regions within specific neural circuitries. ALFF and RSFC have been used to identify the neural mechanisms underlying human cognition, social behavior, and personality in both healthy and clinical populations (Power et al., 2011). Thus, this study aimed to investigate the neural mechanisms underlying trait self-control and the association between trait self-control and overeating from both independent brain activation indexed by ALFF and functional connectivity between brain regions indexed by RSFC.

Epidemiological evidence has shown that eating disorder symptoms are more prevalent in women than in men (Striegelmoore et al., 2009). Especially when encountering stressful events, women are generally likely to engage in excessive and emotional eating than men (Zellner et al., 2006). Such sex differences in eating behaviors may be related to region-specific brain structure and function (Chao et al., 2017; Ruigrok et al., 2014). Previous neuroimaging studies show that women display greater reactivity to food stimuli in the brain regions that have been implicated in emotional processing and reward-seeking (Uher et al., 2006; Wang et al., 2009). Given the prevalence of sex differences in dietary characteristics, a better understanding of the sex differences in brain structure and function could provide insight into related neurophysiological mechanisms and corresponding interventions. Therefore, this study also aimed to further identified sex differences in the neural substrates underlying the relationship between self-control capacity and overeating within the context of the COVID-19 pandemic.

The global spread of COVID-19 has led to an increase in disordered eating among some people with poor coping abilities. In the present study, we examined whether self-control capacity before the outbreak (September 2019, T1) was associated with overeating during the pandemic (February 2020, T2), and revealed the intrinsic brain activity and functional connectivity underlying this association. Based on prior research, we hypothesized that trait self-control (T1) could be negatively associated with overeating tendency (T2) during the pandemic, and expected the neural correlates underlying trait self-control and the association between trait self-control and overeating, to be primarily involved in increased activation in the cognitive and executive control brain regions (e.g., DLPFC, VLPFC) and functional connections, as well as decreased activation in incentive and affective processing brain regions (e.g., OFC, fusiform gyrus) and functional connections.

2. Methods

2.1. Participants and procedure

The data were derived from the Behavioral-Brain Research Project, which is designed to investigate the neuro basis of personality in Chinese young adults. This project used a random method to recruit healthy college students from various departments of a university in Chongqing, China. As showed in Fig. 1, the first wave (T1, September 2019, before the epidemic) obtained personality data and imaging data from 634

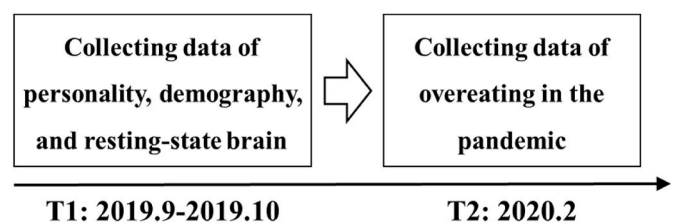


Fig. 1. The flow scheme.

college students. The second wave (T2, February 2020, during the pandemic) obtained eating-related data by following up with 538 students from the original group ($M_{\text{age}} = 18.75$, $SD = 1.56$, range 17–20 years; female: $n = 374$; male: $n = 164$). From T1 to T2, the longitudinal recovery rate was 84.86%. Chi-squared tests and t-tests were used to assess the effect of attrition for gender, age, trait self-control, and overeating, and no significant differences were found between those remained and those excluded (0 = missing, 1 = complete): $\chi^2_{\text{gender}} = 0.56$, $p > 0.05$; $t_{\text{trait self-control}} = -0.003$, $p > 0.05$; $t_{\text{overeating}} = 0.70$, $p > 0.05$; $t_{\text{age}} = 1.65$, $p > 0.05$. All participants signed the informed consent document prior to the experiment and received an honorarium at the end of the study. Ethical approval of this study was granted by the Ethics Committee of the University, and all procedures were in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Measurements

Trait self-control was measured using a brief and well-validated Chinese version of the Self-Control Scale (Tan and Guo, 2008; Tangney et al., 2004) containing 19 items. Participants answered on a five-point Likert scale (e.g. “I am good at resisting temptation”) ranging from 1 (not at all like me) to 5 (very much like me) to indicate their general self-control tendencies. Higher scores on this scale indicated greater self-control capacity. Cronbach’s alpha of trait self-control was 0.88 in the current sample.

Overeating was measured with the Uncontrolled eating, the sub-dimension of Three Factors Eating Questionnaire-R18 (Angl e et al., 2009), which refers to a tendency to overeat with the feeling of being out of control (e.g., “I get so hungry that my stomach often seems like a bottomless pit”). Participants were asked to respond to nine items of uncontrolled eating on a four-point scale (1 = not at all, 4 = very much), with a high score indicating a high tendency to overeat. In the present study, Cronbach’s alpha of overeating was 0.92.

2.3. Resting state fMRI data acquisition and preprocessing

2.3.1. Image acquisition

For each participant, a total of 8 min rsfMRI scanning was performed in a 3T Trio scanner (Siemens Medical, Erlangen, Germany). During the process of scanning, each participant was asked to remain still and relaxed, not open his/her eyes and not think of anything deliberately. Foam pads and earplugs were employed to reduce head motion and scanning noise. We used a gradient echo planar imaging sequence to obtain the resting-state functional image, and the scanning parameters were as follows: repetition time = 2000 ms; echo time = 30 ms; slices = 62; slice thickness = 2 mm; field of view read = 224×224 mm²; flip angle = 90°; resolution matrix = 112×112 ; voxel size = $2 \times 2 \times 2$ mm³; phase encoding direction = PC » AC. Each section contained 240 volumes. High-resolution T1-weighted structural images were acquired from all participants using a 3T Siemens Trio scanner (Siemens Medical, Erlangen, Germany). The 3-D spoiled gradient-recalled sequence used the following parameters: TR = 2530 ms; TE = 2.98 ms; field of view read = 256×256 mm²; flip angle = 7°; base resolution = 256×256 ; slice per slab = 192; slice oversampling = 33.3%; voxel size = $0.5 \times 0.5 \times 1$ mm³; phase encoding direction = AC » PC. The high-resolution T1-weighted structural images provided an anatomical reference for the functional scans.

2.3.2. Image data preprocessing

The Data Processing & Analysis for (Resting-State) Brain Imaging (DPABI, Yan et al., 2016) was used to preprocess the image data. The preprocessing was conducted with the following steps. The first 10 images were discarded to allow for participants’ familiarisation and fMRI signal stabilisation. The remaining images were corrected for temporal shifts between slices, realigned to the middle volume. Next, by using the

EPI templates in SPM12 (Ashburner, 2007), each image volume was spatially normalized to the Montreal Neurological Institute 152-brain template, with a resolution voxel size of $3 \times 3 \times 3$ mm³. The images were then spatially smoothed with a 4-mm full width at half maximum (FWHM) of Gaussian kernel and linear trends were subsequently removed. Then, we regressed nuisance signals including white matter, cerebrospinal fluid, and head motion parameters, and regressed their derivatives using a Friston 24 parameter model to control the effects of potential physiological artifacts (Friston et al., 1996). In addition, linear and quadratic trends were also included as regressors since the BOLD signal exhibits low frequency drifts. To remove the effects of very-low-frequency drifts and high-frequency noises, all images were filtered using a temporal band pass filter (0.01–0.08 Hz) (for RSFC but not for ALFF). Finally, we implemented data scrubbing to better address head motion concerns. The bad time points were regarded as regressors that defined as volumes with framewise displacement (FD) power >0.5 mm as well as the two succeeding volumes and one preceding volume to reduce the spillover effect of head motion. For all participants, none has head motion between volumes in any direction was >3 mm or rotation in any axis >3° during scanning.

2.4. Statistical analysis

2.4.1. ALFF-behavior correlation analysis

The time series in each voxel was transformed to a frequency domain with a fast Fourier transform. Next, the power spectrum was obtained. Then, the square root of the power spectrum was calculated and averaged across 0.01–0.08 Hz for each voxel. This averaged square root was considered to be the ALFF. For standardization purposes, the ALFF value of each voxel was divided by the global mean ALFF value to normalize the global volume effects across subjects (Zang et al., 2007). Calculations were conducted using DPARSF software. To identify the brain regions of spontaneous brain activity related to trait self-control, we employed whole-brain correlation analyses of trait self-control scores and ALFF values of each voxel in the brain, with sex, age, and FD as controlling covariates. To determine statistical significance, the results were corrected for multiple comparisons using the Gaussian random field (GRF) program, and the threshold was set as a corrected cluster $p < 0.05$ (single voxel $p < 0.005$, cluster size >40 voxels). These analyses were conducted using the DPABI software toolbox (<http://rfmri.org/dpabi>, version 2.3) in MATLAB platform.

2.4.2. RSFC-behavior correlation analysis

We performed RSFC-behavior correlation analyses to investigate whether the clusters identified through the ALFF-behavior analyses interacted with other regions to explain self-control ability. To do so, seed regions were created as 6-mm sphere centered on the peak coordinate of the clusters associated with trait self-control. For each participant, we first averaged the time series of all voxels in each seed. We then performed correlation analyses between the mean time series in each seed and that of other voxels in the brain, obtaining participant-level correlation maps. For standardization purposes, the correlation maps were normalized to z maps using Fisher’s r-to-z transformation. In the group-level analyses, we conducted correlation analyses between the z maps and trait self-control scores to detect any association between RSFC and trait self-control, with age and sex as controlling variables. For multiple comparisons correction, we used the GRF program with the threshold setting as a corrected cluster $p < 0.05$ (single voxel $p < 0.005$, cluster size >100 voxels). These analyses above were performed using DPABI software.

2.4.3. Mediation model analysis

To determine whether trait self-control would be associated with overeating through resting-state brain activity and connectivity, we conducted a moderated mediation analysis using SPSS 22.0. Given the sex differences assumed to be present in disordered eating, in the

moderating mediation model, we treated the ALFF and RSFC of brain regions as the mediating variables, trait self-control as the independent variable; overeating as the dependent variable; age, FD, and body mass index (BMI) as covariates; and sex as the moderating variable. The mediating effect was tested by a bootstrapping analysis with 5000 iterations using the SPSS macro PROCESS (Model 7) (Hayes and Scharok, 2013). If the 95% confidence interval (CI) did not contain zero, then the moderating effect was deemed significant.

3. Results

3.1. ALFF-behavior correlation analysis

The descriptive statistics of all measures are presented in Table 1. The kurtosis and skewness values of all variables are between -1 and $+1$, indicating that the data presents a normal distribution.

To reveal the relationship between spontaneous brain activity and self-control ability, we correlated trait self-control with the ALFF of each voxel in the brain. As presented in Fig. 2 and Table 2, after adjusting for sex, age and FD, trait self-control was negatively related to ALFF in the left fusiform gyrus ($r = -0.22, p < 0.0001$) and the left precuneus ($r = -0.22, p < 0.0001$), and positively related to the right DLPFC ($r = 0.20, p < 0.0001$), VLPFC ($r = 0.24, p < 0.0001$), and the left anterior insula ($r = 0.09, p < 0.05$).

3.2. RSFC-behavior correlation analysis

To explore whether the identified brain regions indexed by ALFF interacted with other regions associated with self-control ability, we conducted a correlation analysis between RSFC strength and trait self-control with sex, age, and FD as controlling variables (see Table 3). The analysis showed that trait self-control was negatively correlated with the RSFC strength from the right DLPFC to the orbital frontal gyrus ($r = -0.20, p < 0.0001$), anterior cingulate cortex ($r = -0.23, p < 0.0001$), inferior parietal lobule ($r = -0.20, p < 0.0001$), and posterior cingulate cortex ($r = -0.17, p < 0.0001$). RSFC between the right VLPFC and left anterior cerebellar ($r = 0.20, p < 0.0001$) was found to be positively associated with self-control ability. Trait self-control was also negatively correlated with the FC between the left fusiform gyrus and left temporal pole ($r = -0.20, p < 0.0001$), and the FC from precuneus to insula ($r = -0.21, p < 0.0001$) and anterior cingulate cortex ($r = -0.21, p < 0.0001$).

3.3. Mediation model analyses

Behaviorally, the correlation results showed that trait self-control at T1 was significantly negatively related to overeating at T2 ($r = -0.27, p < 0.01$). Sex difference (male = 1, female = 0) was found in trait self-control and overeating. The level of trait self-control of men was significantly higher than that of women ($M_{\text{male}} = 3.24, M_{\text{female}} = 3.11, t = 2.44, p = 0.015$), while the level of overeating of women was significantly higher than that of men ($M_{\text{male}} = 1.91, M_{\text{female}} = 2.22, t = -5.39, p < 0.01$). Sex differences indicated that the association of trait self-control with overeating might be moderated by sex. We further investigated the associations between resting-state brain activity or connectivity and overeating. Overeating was found to be positively

Table 1

Descriptive statistics of participant-level variables ($N = 538$).

Variable	Mean	SD	Range	Skewness	Kurtosis
TSC	3.15	0.55	1.57–4.63	-0.04	-0.20
Overeat	2.13	0.63	1–4	0.31	0.20
age	19.48	0.86	16–23	0.71	0.85
BMI	20.73	2.56	15.04–30.07	0.71	0.75

Note: N = number; SD = standard deviation; TSC = trait self-control.

Table 2

Brain regions where ALFF were associated with trait self-control.

Region	Cluster Size	BA	MNI Coordinates			
			x	y	z	R
Correlation with ALFF						
Fusiform gyrus(L)	45	19	-45	-78	-3	-.20
DLPFC(R)	117	46	48	48	9	.18
VLPFC(R)	82	44	42	15	15	.20
Anterior insula(L)	124	13	-30	0	21	.23
Precuneus(L)	73	5	-3	-45	60	-.19

Notes: The threshold for significant regions was set at $p < 0.05$ at the cluster level, combined with $p < 0.005$ at the voxel level (GRF program, ALFF analysis: cluster size >40 voxels).

Abbreviations: DLPFC, dorsolateral prefrontal cortex; VLPFC, ventrolateral prefrontal cortex; BA, Brodmann area; MNI, Montreal Neurological Institute; R, right; L, left. ALFF, amplitude of low-frequency fluctuation.

associated with ALFF in the left fusiform gyrus ($r = 0.15, p < 0.01$); and negatively associated with ALFF in the left DLPFC ($r = -0.13, p < 0.01$), VLPFC ($r = -0.14, p < 0.01$), and anterior insula ($r = -0.13, p < 0.01$). These results indicated that a close relationship among trait self-control, overeating, and resting-state brain activity and connectivity.

To examine whether the ALFF and RSFC above could mediate the association of trait self-control at T1 with overeating at T2, we conducted a moderated mediation analysis with trait self-control as the independent variable; ALFF in the brain and RSFC as mediating variables; overeating as the dependent variable; age, BMI and FD as covariates, and sex as moderating variable. As depicted in Fig. 3, a significant direct path was found from trait self-control at T1 to overeating at T2 (direct effect coefficient = $-0.25, SE = 0.04, 95\% CI = [-0.33, -0.16]$). A significant indirect path was also found from trait self-control to overeating through the fusiform gyrus (indirect effect coefficient = $0.02, SE = 0.01, 95\% CI = [0.003, 0.049]$). There was a significant main effect ($\beta = -0.15, SE = 0.04, 95\% CI = [-0.22, -0.08]$) of trait self-control and an interaction effect ($\beta = 0.09, SE = 0.04, 95\% CI = [0.02, 0.16]$) of trait self-control \times sex on ALFF in the fusiform gyrus. To specify the interaction patterns, the significant interaction effects were plotted by simple slopes of trait self-control at high ($+1$ SD) and low (-1 SD) levels and sex (see Fig. 3). Simple slope analysis showed that trait self-control was negatively associated with ALFF in the fusiform gyrus in female participants ($\beta = -0.25, t = -4.91, p < 0.0001$) but not in male participants ($\beta = -0.02, t = -0.30, p > 0.05$). This result suggested that only women with higher trait self-control could regulate overeating through decreased activation of fusiform gyrus.

Moreover, as depicted in Fig. 4, a significant indirect path was also found from trait self-control to overeating through DLPFC (indirect effect coefficient = $-0.02, SE = 0.01, 95\% CI = [-0.06, -0.001]$). There was a significant main effect ($\beta = 0.16, SE = 0.04, 95\% CI = [0.08, 0.24]$) of trait self-control and an interaction effect ($\beta = 0.13, SE = 0.04, 95\% CI = [0.05, 0.20]$) of trait self-control \times sex on ALFF in the DLPFC. Simple slope analysis showed that trait self-control was positively associated with ALFF in the right DLPFC in both male ($\beta = 0.27, t = 3.58, p < 0.01$) and female participants ($\beta = 0.11, t = 2.08, p < 0.05$). This result suggested that both women and men with higher trait self-control could regulate overeating through increased activation of the DLPFC, although this association was stronger for men than women.

4. Discussion

During the COVID-19 pandemic, individuals are at risk of developing or exhibiting disordered eating behaviors (Rodgers et al., 2020). The present study utilized rsfMRI data to examine how trait self-control and its neural basis at baseline (T1) in a sample of college students ($N = 538$) was associated with overeating propensity during the pandemic six months later (T2). As predicted, the findings showed that trait self-control at T1 was directly and negatively associated with overeating

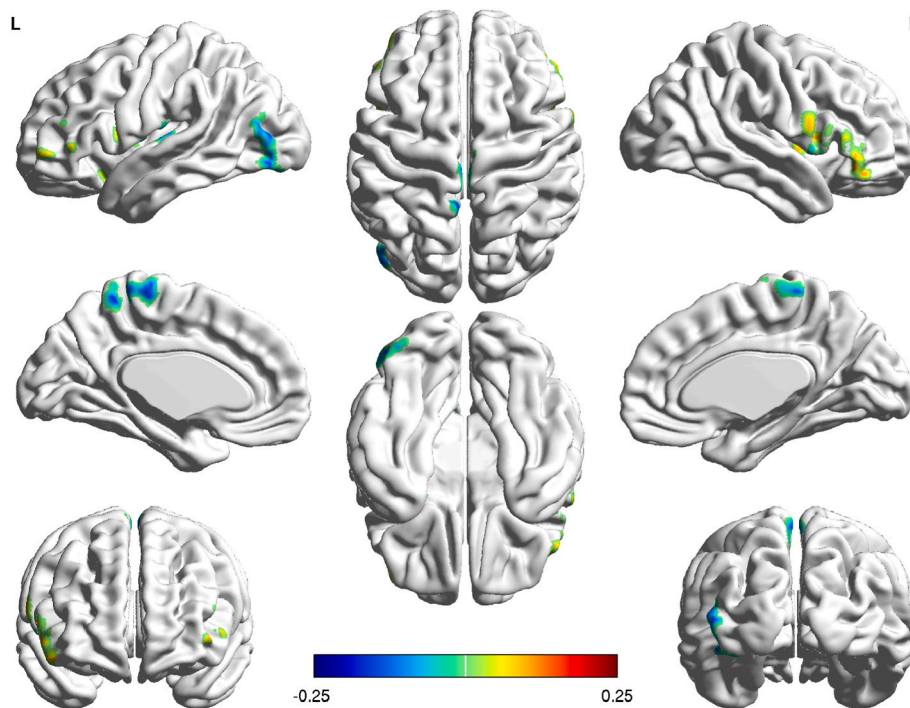


Fig. 2. Brain regions associated with trait self-control. After controlling for age, sex and FD, trait self-control was positively associated with the ALFF in the right DLPFC, VLPFC, and the left anterior insula; and negatively associated with the ALFF in the left fusiform gyrus and precuneus gyrus.

Table 3
Brain regions where RSFC were associated with trait self-control.

Seed Region	Region	Cluster Size	BA	MNI Coordinates			R
				x	y	z	
Correlation with RSFC							
Fusiform gyrus(L)	Temporal pole (L)	135	38	-45	21	-21	-.22
DLPFC(R)	Frontal orbital cortex(L)	108	47	-30	21	-24	-.18
	Anterior cingulate cortex(L)	584	9/10	-6	33	27	-.21
VLPFC(R)	Anterior cerebellar(L)	113	18	-27	-48	-27	.18
Precuneus (L)	Insula(L)	119	13	-33	6	-3	-.19

Notes: The threshold for significant regions was set at $p < 0.05$ at the cluster level, combined with $p < 0.005$ at the voxel level (GRF program, RSFC analyses: cluster size >100 voxels). RSFC, resting-state functional connectivity.

at T2, which was consisted with previous studies showing that individuals with high self-control capacity could effectively resist food cravings (Gillebaart et al., 2016) and maintain healthy eating patterns

(Allom and Mullan, 2014). The present study revealed the importance of trait self-control in alleviating disordered eating behaviors during the COVID-19 pandemic.

Whole-brain correlation analyses revealed that individuals with higher trait self-control showed enhanced ALFF in the DLPFC, VLPFC, and anterior insula in the lateral prefrontal network, which has been implicated in tasks requiring executive control, goal maintenance, emotional regulation, and response inhibition (Aron et al., 2014; Levy and Wagner, 2011; McClure and Bickel, 2014). Additionally, individuals with greater self-control capacity also showed decreased ALFF in the fusiform gyrus and precuneus gyrus. The fusiform gyrus in the occipito-temporal area is typically associated with object and face recognition (Karnath et al., 2009). Previous studies have indicated that the fusiform gyrus may extend beyond simple recognition and can be implicated in emotional processing and incentive behaviors (Radua et al., 2014; Uher et al., 2006). Moreover, previous research based on task and resting fMRI showed that the precuneus is also implicated in emotional function (Chang et al., 2014). The results of the resting brain regions as indexed by ALFF demonstrated that high trait self-control was associated with increased activation of cognitive-controlled brain regions and decreased activation of brain regions associated with incentive- and emotion-processing. Generally, individuals with high trait self-control are more likely to adhere to long-term goals than those

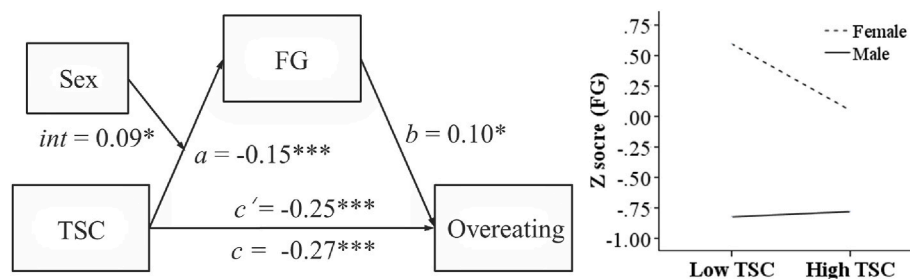


Fig. 3. The moderating mediation model and the simple slope effect. The mediating effect of FG in the association between trait self-control and overeating was moderated by sex. TSC, trait self-control; FG, fusiform gyrus.

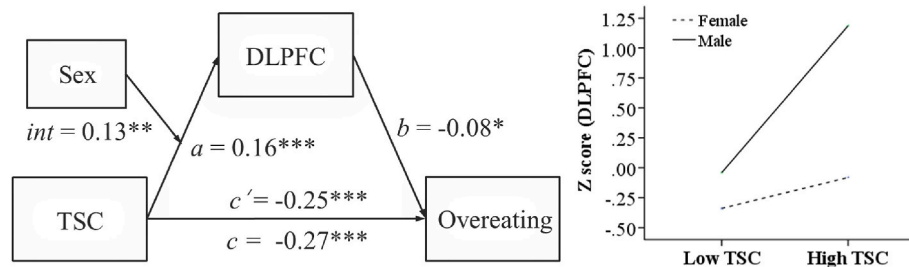


Fig. 4. The moderating mediation model and the simple slope effect. The mediating effect of DLPFC in the association between trait self-control and overeating was moderated by sex. TSC, trait self-control; DLPFC, dorsolateral prefrontal cortex.

with low trait self-control. The ALFF results suggest that individuals with high trait self-control are more likely to show goal maintenance and execution and less likely to be affected by incentive and emotional processing.

The traditional conceptualization of self-control is that it enables an individual to effortfully overcome unhealthy desires or impulses to achieve valued long-term goals (De Ridder et al., 2012). Increasing evidence suggests that individuals with high trait self-control have healthier habits and enact goal-consistent behavior with less effort (De Ridder and Gillebaart, 2017; Galla and Duckworth, 2015). The RSFC results showed that trait self-control was associated with decreased functional connectivity between the DLPFC and orbitofrontal cortex and anterior cingulate cortex. The OFC is associated with impulsive behaviors, reward-encoding, and hedonic pursuit (Kringelbach, 2005; McClure et al., 2004). And the anterior cingulate cortex is associated with conflict monitoring and cognitive control signaling (Kerns et al., 2004). Our results might provide neuroimaging evidence that individuals with higher trait self-control were more likely focus on long-term goals rather than immediate rewards. Furthermore, trait self-control was associated with decreased connectivity of the fusiform gyrus-temporal pole and the precuneus-insula. Located in the limbic and paralimbic areas, the temporal pole and insula are important regions underlying coding for affective and incentive processes (Cavanna and Trimble, 2006; Craig, 2009), and increased activation in these regions could increase the risk for overeating and future weight gain (Gupta et al., 2018). Decreased connectivity of these regions suggest that individuals with high trait self-control could improve cognitive function by downregulating irrational mental simulation.

We also found that increased connectivity between the right VLPFC and anterior cerebellar was associated with trait self-control. The anterior region of the cerebellum is commonly involved in simple and complex motor performance (Akhlaghi et al., 2012; Ullen et al., 2003). Previous research indicates that in response to eating meals, successful dieters have greater activation in the DLPFC and anterior cerebellar, compared to non-dieters (Delparigi et al., 2007). The increased fronto-cerebellar connection might reflect greater executive control over actions in those with high trait self-control. Taken together, these findings from ALFF and RSFC support the dual-system model and indicate that trait self-control engaged a widespread brain regions and connections that implicated in not only behavioral inhibition and cognitive control in the control system but also emotional processing and incentive behavior in the affective system.

The sex differences in behavioral performance and neural mechanisms are well documented (Hines, 2010; Tunc et al., 2016). In the present study, the moderated mediation models further verified sex differences in the neural substrates (indexed by ALFF) underlying the association between trait self-control and overeating. First, both male and female individuals with high trait self-control were associated with increased activity in the DLPFC, which could be associated with low levels of overeating during the COVID-19 pandemic. This finding is in line with previous studies showing that greater DLPFC activation was associated with higher levels of self-control during food-related

decision-making in healthy-weight dieters (Hare et al., 2009). Second, ALFF in the fusiform gyrus could mediate the association between trait self-control and overeating in women. Previous studies indicate that compared to men, women are more likely to have disordered eating and obesity (Gupta et al., 2018), eat more when under stress (Zellner et al., 2006), and have more impulsive and frequent cravings (Cepedabenito et al., 2003). The lower activation of fusiform gyrus suggests that women with high trait self-control experienced less emotional and incentive problems, and then showed healthy eating pattern. Taken together, these findings suggest that women with high self-control capacity could alleviate overeating during the COVID-19 pandemic by regulating brain regions involved not only in cognitive control but also affective processing, while men with high trait self-control are more likely to depend on executive control brain regions to resist overeating.

Existing studies demonstrate that neurophysiological interventions can promote self-control capacity. Studies indicate the modulating brain activity using non-invasive brain stimulation, such as transcranial direct current stimulation has been shown to reduce food craving and food consumption in both healthy and disordered eating populations (Sedgmond et al., 2019). Moreover, sex differences in the human brain are essential to understanding anatomical foundation and development in the brain, and further offer important considerations for personalized medicine and interventional strategies (Gupta et al., 2018; Tunc et al., 2016). The present findings suggest that the neural intervention target should be in the cognitive and executive control brain regions for men, while for women, the targeted regions should be those associated with cognitive control and emotional processing.

Despite its implications, the limitations should be acknowledged. First, the participants were recruited from a population of healthy Chinese young adults, which may limit the generalizability of our findings. Considering that the pandemic's influence may vary in different populations, future research is needed to validate our findings among more diverse populations across different ages and, careers as well as in samples with dieting goals or disordered eating symptoms. Second, measurement limitations include using brief self-report measures to assess eating- and trait-related constructs, which were vulnerable to subjectivity. Multiple measurements with ecological validity, such as third-party report, changes in weight, and experience sampling methods should be considered in future research. Meanwhile, the present study did not collect and control overeating tendency at pre-pandemic and other variables affecting overeating during the pandemic, so we could not determine the causal association of self-control ability with overeating.

The current study investigated the resting state neural correlates underlying the relationship between trait self-control and overeating during the COVID-19 pandemic. Neuroimaging results indicated that individuals with high trait self-control exhibited increased activation in brain regions associated with cognitive control and executive control and reduced activity in affective and incentive processing regions. The RSFC results showed that trait self-control was associated with decreased connectivity in brain regions associated with reward-encoding, conflict monitoring, and emotional processing, and

increased connectivity in the motor regulation region. Furthermore, the longitudinal mediation models showed that higher self-control ability could be associated with lower overeating during the pandemic, and there were sex differences in neural correlates underlying this association. These findings may have practical implications for neural intervention programs that aim to strengthen self-control ability.

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Data availability statement

Data can be found from DOI: 10.13140/RG.2.2.17603.53281.

Authors contributions

Qingqing Li: Conceptualization, Data curation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing; Guangcan Xiang: Visualization, Methodology, Formal analysis, Writing – original draft; Shiqing Song and Yong Liu: Data curation, Methodology, Formal analysis; Hong Chen: Conceptualization, Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of competing interest

All co-authors have approved the manuscript, and there are no conflicts of interest to declare.

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