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RESEARCH ARTICLE

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Altered motivation of effortful decision-making for self and others in subthreshold depression

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Abstract

Background: Amotivation is a typical feature in major depressive disorders and refers to individuals exhibiting reduced willingness to exert effort for rewards. However, the motivation pattern when deciding whether to exert effort for self versus others in people with depression remains unclear.

Methods: We conducted a functional magnetic resonance imaging study and employed an adapted Effort-Expenditure for Rewards Task in subthreshold depressive (SD) participants ($n = 33$) and healthy controls (HC) ($n = 32$). This required participants to choose between a fixed low-effort/low-reward and a variable high-effort/high-reward option, and then immediately exert effort to obtain corresponding rewards for themselves or for unfamiliar people.

Results: Compared with the HC group, the SD group showed blunted activity in the left dorsal anterior cingulate cortex/dorsomedial prefrontal cortex, bilateral anterior insula (AI), and right putamen-left dorsolateral prefrontal cortex functional connectivity when choosing to exert effort for themselves. Additionally, the SD group exhibited increased willingness and greater activation in the bilateral AI when choosing to exert effort for others. Furthermore, these brain activations and functional connectivity were positively related to self-reported motivation.

Conclusions: These findings show altered motivation during effort-based decision-making in individuals with the mild depressive state, particularly with higher motivation for others. Thus, this suggests that motivational behaviors and prefrontal–striatal circuitry are altered in individuals with SD, which can be utilized to discover treatment targets and develop strategies to address mental illness caused by motivation disorders.

KEYWORDS

anterior insula, dorsolateral prefrontal cortex, dorsomedial prefrontal cortex, effort, motivation, others, reward, self, subthreshold depression

1 | INTRODUCTION

Motivational deficit accompanied by limited anticipatory pleasure is a typical feature of depression (Sherdell et al., 2012; Treadway & Zalda, 2011; Ubl et al., 2015; D. Zhang et al., 2020), which results in patients' impairments in social and life functioning (Horne et al., 2021; National Institute of Mental Health, 2019; Pietrzak et al., 2012). Motivation is goal-directed and the term *effort*, which refers to the intensification of physical or mental activities needed to obtain desired outcomes (Grahek et al., 2019; Inzlicht et al., 2018), is a central concept in motivation studies (Braver et al., 2014; Grahek et al., 2019). To this end, the ability to weigh the costs and benefits during effort-based decision-making is critical for optimal goal-directed behaviors (Lopez-Gamundi et al., 2021). Behavioral evidence has shown that people with major depressive disorder (MDD) and subthreshold depression (SD) are less willing to make effortful choices than healthy controls (HCs), and this motivational deficit predicts decreased anticipatory pleasure and prolonged depression episodes (Cléry-Melin et al., 2011; Hershenberg et al., 2016; Sherdell et al., 2012; Tran et al., 2021; Treadway et al., 2012; Yang et al., 2014).

Although the importance of motivation and effort is evident, little is known about the neural mechanisms of effort-based decision-making in depression. Yang et al. (2016) adopted a frequently used task—Effort-Expenditure for Rewards Task (EEfRT; Treadway et al., 2012)—to investigate the neural response of effort-based decision-making in MDD. During this task, participants were required to make a choice between a fixed low-effort/low-reward baseline and a variable high-effort/high-reward option and, subsequently, exert the selected effort to obtain its combined reward. The results found that, compared with HCs, MDD patients were less willing to choose a high-effort/high-reward offer, and their caudate nucleus showed reduced activation as a function of effort/reward magnitude (Yang et al., 2016). Recently, the same group used EEfRT and found that MDD patients showed weaker functional connectivity between the caudate and the cingulate gyrus with increase in reward magnitude (Wang et al., 2022). Besides these pioneering works, we found two related studies involving effort processing in depression (Park et al., 2017; Rzepa & McCabe, 2019). However, these two studies did not require participants to make a choice between high or low level of effort; thus, their findings did not provide knowledge of changed motivational and effortful decision-making in depression.

Another literature gap prompting this study is the *recipient* of effortful decision-making. People can exert effort not only for self, but also for others. However, most studies only examined the former condition; thus, it is unclear how motivation changes when exerting effort for others. While depressed individuals show impaired self-relevant processing, such as inappropriate self-blame, negative self-evaluation, excessive self-criticism, and reduced positive self-biases compared with HCs (Auerbach et al., 2014, 2015; Hobbs et al., 2021), they often show higher prosocial actions due to their pathologically increased guilt (O'Connor et al., 2000, 2011). Thus, we hypothesize that this may result in enhanced motivation to exert effort for others. Distinguishing between the motivation of making effortful choices for self and others in individuals with depression would help determine the following: (1) the nature of impaired motivation in depression and (2) the appropriate boundary for clinical treatment of patients' motivational deficits. Recently, several behavioral studies revealed enhanced motivation to exert effort for themselves than for others in healthy young populations (Lockwood et al., 2017, Lockwood, Abdurahman, et al., 2021). However, until now, no study has addressed motivation processing when expending effort to benefit themselves versus others in individuals with depression.

Using EEfRT and relative paradigms, studies have demonstrated that motivation during effort-based decision-making for oneself is subserved by a brain network including the dorsal anterior cingulate cortex (dACC)/dorsomedial prefrontal cortex (DMPFC), anterior insula (AI), and striatum (Chong et al., 2017; Lopez-Gamundi et al., 2021; Massar et al., 2015). Specifically, the dACC/DMPFC and AI are often coactivated to guide the effort-reward trade-off (Arulpragasam et al., 2018; Hauser et al., 2017; Klein-Flügge et al., 2016) and lesions to the dACC or DMPFC resulted in decreased preference for high effort choices (Walton et al., 2002, 2009). In addition, the ventral striatum encodes the subjective value of choice options (Aridan et al., 2019; Arulpragasam et al., 2018; Croxson et al., 2009; Hauser et al., 2017), whereas the dorsal parts of the striatum, especially the motor-related area—putamen, represents physical-related effort costs (Burke et al., 2013; Kurniawan et al., 2013). Previous studies suggest that neural processing in these brain areas comprise dysfunctional anticipation/motivation-related reward processing (Pizzagalli et al., 2009; Rzepa & McCabe, 2019; Smoski et al., 2009) in depressed populations. Therefore, the present study will focus on these brain regions to further investigate group differences in the anticipatory (choice) phase during effort-based decision-making.

This study used EEfRT to investigate neural responses of motivation for the self and an unfamiliar other underlying effortful decision-making in individuals with SD. Given that SD has been considered a developmental prodrome to MDD (Dotson et al., 2021; Wesselhoeft et al., 2013), focusing on people with SD could contribute to developing preventive interventions, as well as rule out the effect of clinical treatments (e.g., antidepressant medications) on the motivation and reward processing (He et al., 2019). We focused on neural activity changes in the choice phase between the SD and HC groups as it represents a cost–benefit trade-off between effort costs and potential rewards (Klein-Flügge et al., 2016; Scholl et al., 2015). As depressive individuals have shown impaired motivational effort decision-making and self-relevant processing relative to the healthy population (Hobbs et al., 2021; Horne et al., 2021), we hypothesize that SD would show less effortful motivation under the "effort for self" condition. Based on the blunt activity in the dACC/DMPFC, insula, and dorsal striatum in individuals with depression (Pizzagalli et al., 2009; Rzepa & McCabe, 2019; Smoski et al., 2009), as well as the critical functions of these regions in effort-based decision-making (Klein-Flügge et al., 2016; Kurniawan et al., 2013), we further expect that the activation and functional connectivity pattern of these brain areas would be altered during effortful decisions for self in SD. Moreover, as limited literature involving effortful decision-making for others in depressed populations exists, we did not develop clear hypotheses under the "effort for other" condition.

2 | METHODS

2.1 | Participants

The Beck Depression Inventory Second Edition (BDI-II: Beck et al., 1996) was administered to approximately 500 undergraduate students from Shenzhen University. According to the norms of the BDI-II, students who scored >13 were assigned to the SD group and those who scored ≤13 were assigned to the HC group (Beck et al., 1996). Participants were excluded according to the following criteria: (1) neurological disorders and any lifetime Axis I disorders according to structured clinical interview for DSM-IV Axis I Disorders, Non-Patient edition (First et al., 2002); (2) seizure disorder; (3) self-reported use of any psychotropic substances, especially antidepressants; (4) current alcohol or drug dependence. Finally, 65 right-handed subjects (33 SD and 32 HC) were invited to participate in the functional magnetic resonance imaging (fMRI) experiment. Two individuals were excluded due to excessive head movement (>2.5 mm in translation or >2.5° in rotation) during the scanning, leaving 63 participants (33 SD and 30 HC) for fMRI analyses (Table 1). The study was approved by the Ethics and Human Protection Committee of Magnetic Resonance Imaging Center from Shenzhen University. All participants provided informed consent before the experiment.

2.2 | Self-reported measures

At the date of the experiment, participants completed three questionnaires before scanning: (1) the Self-Rating Depression Scale (SDS: Zung, 1965) measures depressive symptoms, with a higher score indicating higher depressive severity (range = 0.25–1); (2) the TEPS-ANT subscale of Temporal Experience of Pleasure Scale (TEPS: Gard et al., 2006) measures the anticipatory component of pleasure experience, with a higher score of anticipatory pleasure indicating stronger feelings of wanting and is correlated with greater motivation and goal-directed behaviors (range = 10–60); (3) the BAS-Drive subscale of Behavioural Inhibition/Activation Scale (BIS/BAS: Carver & White, 1994) measures motivation of behavioral approach, with a higher score indicating a greater tendency to actively pursue appetitive or desired goals (range = 1–16).

Sample characteristics are reported in Table 1. The SD and HC groups did not differ in terms of age, gender and handedness. Participants in the SD group reported significantly higher depressive symptoms (SDS). Compared with the HC group, the SD group also reported significantly lower anticipatory pleasure (TEPS-ANT) or approach motivation (BAS).

2.3 | Procedure and experimental design

Participants first practiced and familiarized themselves with the effort-based decision-making task (described below). Subsequently, they underwent one run of T1-weighted structural scan and performed four runs of the in-scanner effort task. According to their task performance, the participants received ¥80–110 (approximately $12.4–17.0) at the end of the experiment.

2.3.1 | Effort-based decision-making task

The paradigm used in the present study was modified from the EEfRT (Treadway et al., 2012), which required participants to choose between a high-effort/high-reward and a low-effort/low-reward option on each trial and exert physical effort to obtain a monetary reward. As shown in Figure 1, participants were presented with a choice between two options illustrated by the pie chart, with 1 blue sector indicating a low-effort/low-reward option and 5 or 10 blue sectors indicating a high-effort/high reward option. For the low-effort/low-reward option, participants were required to press the right button on the response box 10 times (20% effort level) with their right thumb within 3 s, which would result in ¥1 on each trial if they successfully achieved the required effort. For the high-effort/high-reward option, participants were required to press the button

TABLE 1 Demographic characteristics (mean and standard deviation)

Items	Subthreshold (SD)	Control (HC)	Statistics[a]
Sample size	33	30	$\chi^2_{(1)} = 0.00$, $p = 1.000$
Gender (male/female)	10/23	13/17	$\chi^2_{(1)} = 1.15$, $p = .283$
Age	20.73 (2.20)	20.23 (1.70)	$t_{(61)} = 0.99$, $p = .325$
Handedness (right/left)	33/0	30/0	
SDS	0.59 (0.08)	0.39 (0.07)	$t_{(61)} = 10.63$, $p < .001$
TEPS-ANT	39.42 (7.28)	46.68 (6.94)	$t_{(61)} = -3.96$, $p < .001$
BAS-Drive	11.79 (2.03)	13.11 (2.08)	$t_{(61)} = -2.50$, $p = .015$

Abbreviations: BAS-Drive, the drive subscale of Behavioural Inhibition/Activation Scale; SDS, the Self-Rating Depression Scale; TEPS-ANT, the anticipatory dimension of Temporal Experience of Pleasure Scale.

[a] χ^2 test was performed on categorical variables. Independent samples *t*-test was performed on continuous variables, with group as the fixed factor.

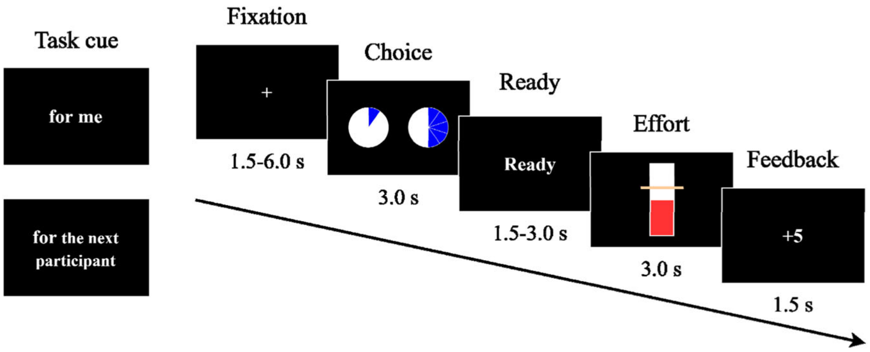

FIGURE 1 Effort-based decision-making task. Each run begins with a task cue, indicating participants were earning rewards for themselves or others. In the scanner, participants were required to choose between a fixed low-effort/low-reward and a variable high-effort/high-reward option. After the decision, they exerted immediately physical effort by repeatedly pressing the button within 3s, during which the red area increased as a function of button presses. The corresponding reward was given if the button presses successfully achieved the effort requirement (shown as a horizontal yellow bar in the screen); otherwise, no reward (¥0) was given.

15 (50% effort level) or 20 times (100% effort level) within 3 s and would win ¥5 or ¥10 if they successfully achieved the required effort. Participants were presented with "+0" in the feedback phase if they failed the task. The number of button presses was set based on our pre-experiment test with 20 subjects which showed that 20%, 50%, and 100% of most undergraduate students' maximum button press number within 3 s was 10, 15, and 20, respectively.

The study was a 2 *group* (SD/HC) × 2 *recipient* (self/other) × 2 *effort/reward* (high/low) design. The *group* was the between-subject factor and the *recipient* and *effort* were the within-subject factors. At the beginning of the effort-for-self run, participants were instructed as follows: "In this section, the obtained reward after successfully completing the task would be given to you." At the beginning of the effort-for-other run, participants were instructed as follows: "In this section, the obtained reward after your successfully completing the task would be given to the next participant." To ensure participants believed that their choices and effort made would truly result in changes in payment for an unfamiliar person, they were informed, before the experiment, of the amount of money the last participant earned for them. This amount ranged from ¥20 to ¥25, randomly assigned to each participant, which would be paid at the end of the experiment. The effort task was divided into four runs, with two "self" and two "other" runs. The order of runs was equal across the two groups and counterbalanced within each group. The left/right side of the presentation of the high/low-choice pie was counterbalanced across trials. Each run lasted 7.5 min and consisted of 32 trials (16 trials for 20% vs. 50% and another 16 trials for 20% vs. 100% effort level). Trials were presented in a fixed-randomized order.

2.3.2 | Postscanning task

Participants were required to rate the following questions on a scale from 1 (extremely disbelieved) to 7 (extremely believed): "How much do you believed that you were earning rewards for yourself?" and "How much do you believed that you were earning rewards for the next participant?". No participants reported a disbelief in the task set, and no difference was observed between the SD and HC groups in the belief rating for self ($t_{(61)} = -0.247$, $p = .806$; 5.52 ± 0.92 vs. 5.57 ± 0.57), or the belief rating for others ($t_{(61)} = 0.146$, $p = .884$; 5.24 ± 0.79 vs. 5.21 ± 0.65).

2.4 | Behavioral and fMRI data acquisition

Stimulus presentation and response acquisition were implemented using E-prime3.0. Participants completed the effort-based decision-making task using an MR-compatible two-button response box. We placed inflatable pads around participants' heads and put medical tape on their forehead to minimize head motion.

fMRI data were collected in a 3 Tesla Siemens Prisma scanner equipped with a 64-channel head coil at the Magnetic Resonance Imaging Center at Shenzhen University. At the start of the imaging session, a high-resolution T1 structural image was acquired with the following sequence parameters: voxel size = 1.1 × 1.1 × 1.1 mm^3, repetition time (TR) = 1.9 s, echo time (TE) = 2.23 ms, flip angle (FA) = 8°, field of view = 220 × 220 mm^2. Functional (T2*-weighted) volumes were collected using a multiband sequence with the following sequence parameters: voxel size = 2 × 2 × 2 mm^3, TR = 1.5 s, TE = 30 ms, FA = 75°, field of view = 192 × 192 mm^2, 72 slices with interleaved multislice mode.

2.5 | Data analysis

Data were preprocessed and analyzed using SPM12 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London; https://www.fil.ion.ucl.ac.uk/spm). Preprocessing included correction for slice timing, realignment estimation and reslicing, coregistration to the individual's high-resolution T1 structural image, normalization to Montreal Neurological Institute space with a spatial resolution of 2 × 2 × 2 mm^3, and spatial smoothing using a Gaussian kernel with a 6 mm full-width at half-maximum.

2.5.1 | Whole-brain analysis

For the effort-based decision-making task, the first subjective-level general linear model (GLM) included four regressors based on each subject's decisions (offered choice presentation onsets for self-high, self-low, other-high, and other-low choices). We also included motion parameters and high-pass filter parameters as additional nuisance regressors. To examine the main effects of *group*, *recipient*, *effort*, and their interactions, four contrasts were computed for each participant: self-high, self-low, other-high, and other-low. The contrast (self-high > self-low) was also included for subsequent psychophysiological interaction (PPI) analysis. First-level SPM contrast images as a parametric modulator were input into a second-level, full-factorial random effects analysis of variance (ANOVA) with pooled variance, with *group* (SD vs. HC) as a between-subjects variable and *recipient* (self vs. other) and *effort* (high vs. low) as two within-subjects variables. *F*-contrasts were applied at the second level to look for significant main effects or interactions, and *T*-contrasts were subsequently performed to illustrate recruited areas in different conditions at the level of the whole brain. For whole-brain and PPI analysis, we set the false discovery rate (FDR) cluster-corrected threshold as $p < .05$ and cluster size threshold as 10 voxels. To determine significance, we also set the family-wise error cluster-corrected threshold as $p < .05$ and cluster size threshold as 10 voxels after performing the permutation test with Threshold Free Cluster Enhancement (Supporting Information: Parts 4 and 5). The main results are consistent between the two correction methods.

2.5.2 | Region of interest (ROI) analysis

To further examine the interaction effect of *group* × *recipient*, we performed ROI analysis. The ROIs of the left DMPFC and bilateral AI were derived from peak cluster of active areas in the *T*-contrast (HC [self] – HC [other] > SD[self] – SD [other]) based on the whole-brain analysis (see Supporting Information: Table S3). Subsequently, we used the MarsBaR (http://marsbar.sourceforge.net) toolbox for SPM to extract beta values. These extracted values were entered into SPSS (IBM, SPSS, version 22) for repeated ANOVA and estimation of effect sizes.

2.5.3 | Functional connectivity analysis (PPI)

Considering that the SD group showed reduced neural activation in reward and motivation-related brain regions in the "self" conditions, we further explored whether there were differences in functional connectivity during effortful decision-making in the self condition between the two groups. For this purpose, we performed PPI analysis on self-run data. We used the right putamen (intersection of the peak cluster in whole-brain analysis and AAL structure) as the seed region since this brain area was the peak area of activation with the greatest cluster size in the contrast (high [self] > low [self]). Given that the interaction effect was observed in the left DMPFC and AI, we also used these regions as seeds. For each participant, the mean time series for the seed region were extracted and data adjusted using the *F*-contrast. Each GLM design matrix included the following PPI regressors: (1) the main effect of seed-region activity, corresponding to PPI.Y; (2) the main effect of the contrast of high [self] > low [self] corresponding to PPI.P; and (3) their interaction, corresponding to PPI.ppi. We also entered the six head-motion parameters into the GLM as covariates. Low-frequency drifts in signal were removed using a high-pass filter with a cutoff at 128 s. After model estimation, the PPI.ppi regressor for the contrast of high [self] > low [self] was entered into a random-effects analysis for all participants.

3 | RESULTS

3.1 | Behavioral results

To probe the differences of willingness to exert effort for the self and an unfamiliar other between the SD and HC groups, we examined the

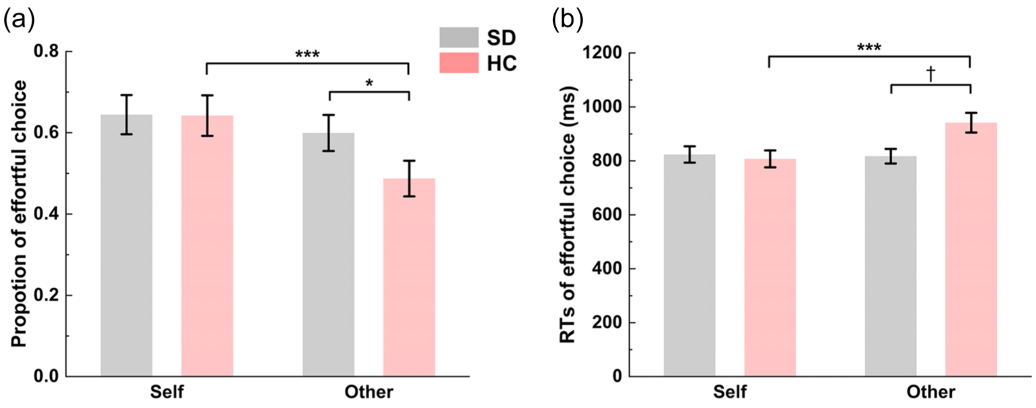

FIGURE 2 Proportion of effortful choice. (a) Proportion of high-effort/high-reward choices during effortful decision-making for self and others between the subthreshold depressive (SD) group and the healthy control (HC) group. (b) Reaction times of choosing high-effort/high-reward options during effortful decision-making for self and others between SD and HC groups. Bars represent one standard error. $^{\dagger}p < .1$, $^{*}p < .05$, $^{***}p < .001$.

proportion of trials (Figure 2a) and reaction times (Figure 2b) in which participants chose the high-effort/high-reward options.

3.1.1 | Proportion of effortful choice

A two-way repeated-measures ANOVA with 2 *group* (SD/HC) × 2 *recipient* (self/other) as factors revealed a significant main effect of *recipient* ($F_{(1,\ 63)} = 15.66$, $p < .001$, $\eta^2_p = 0.199$): the participants were more likely to make effortful choices for self than others (0.643 ± 0.023 vs. 0.543 ± 0.025; mean ± SE). We found a significant interaction of *group* × *recipient* ($F_{(1,\ 63)} = 4.73$, $p = .033$, $\eta^2_p = 0.070$): the SD group were more willing to exert effort for others compared with the HC group ($F_{(1,\ 63)} = 4.91$, $p = .030$, $\eta^2_p = 0.072$; SD vs. HC $= 0.599 \pm 0.036$ vs. 0.487 ± 0.036), while the group effect was not found when required to exert effort for self ($F_{(1,\ 63)} = 0.01$, $p = .960$, $\eta^2_p < 0.001$; SD vs. HC $= 0.644 \pm 0.033$ vs. 0.642 ± 0.033). Another direction of simple effect analysis indicated that the HC group were more willing to exert effort for self than for others ($F_{(1,\ 63)} = 18.52$, $p < .001$, $\eta^2_p = 0.227$), while this recipient effect was not found in the SD group ($F_{(1,\ 63)} = 1.61$, $p = .209$, $\eta^2_p = 0.025$).

3.1.2 | Reaction times of effortful choice

A two-way repeated-measures ANOVA with *group* and *recipient* as factors revealed a significant main effect of *recipient* ($F_{(1,\ 63)} = 5.65$, $p = .021$, $\eta^2_p = 0.081$): the participants made effortful choices faster for self than others (823.4 ± 24.8 vs. 867.3 ± 23.2 ms). We found a significant interaction of *group* × *recipient* ($F_{(1,\ 63)} = 5.72$, $p = .020$, $\eta^2_p = 0.082$): the SD group responded faster when making effortful decisions for others compared with the HC group ($F_{(1,\ 63)} = 2.97$, $p = .090$, $\eta^2_p = 0.044$, marginal significant; SD vs. HC $= 827.3 \pm 31.8$ vs. 907.3 ± 33.8 ms), while the group effect was not significant when making effortful decisions for self ($F_{(1,\ 63)} = 0.03$, $p = .868$, $\eta^2_p < 0.001$; SD vs. HC $= 827.6 \pm 34.0$ vs. 819.3 ± 36.1 ms). Another direction of the simple effect analysis indicated that, the HC group made faster effortful decisions for self than others ($F_{(1,\ 63)} = 10.71$, $p = .002$, $\eta^2_p = 0.143$), but this recipient effect was not significant in the SD group ($F_{(1,\ 63)} < 0.001$, $p = .991$, $\eta^2_p < 0.001$).

3.2 | Whole-brain analysis results

At the second-level analysis, the full-factorial random effects ANOVA with 2 *group* (SD/HC) × 2 *recipient* (self/other) × 2 *effort* (high/low) showed significant main effects of *effort* and *recipient*, a two-way interaction of *group* × *recipient* and a two-way interaction of *recipient* × *effort*. The full results of *T*-contrast are reported in the Supportng Information: Materials (Part 1). In brief, we observed increased activities at the superior frontal gyrus (SFG) during high effortful decision-making in both the self and other conditions (*T*-contrast: high > low, Supporting Information: Table S1 and Figure S1); increased activities at the caudate and medial SFG when making effortful decision for unfamiliar others (*T*-contrast: other > self, Supporting Information: Table S2); reduced activities at the DMPFC and insula during making effortful decisions for self in the SD group (*T*-contrast: HC [self] – HC [other] > SD [self] – SD [other], Supporting Information: Table S3 and Figure S2); and increased activities at the precuneus, medial orbital frontal gyrus, and medial SFG when making high effortful decisions for self (*T*-contrast: high [self] – high [other] > low [self] – low [other], Supporting Information: Table S4).

To perform PPI analysis, we also ran the contrast of high [self] > low [self] at the whole-brain level, resulting in activated brain regions at the right putamen (peak: [24, 8, −2], $k = 138224$) and left caudate (peak: [−18, −14, 24], $k = 28$).

3.3 | ROI results

To further explore the group effects, we extracted the beta values of the ROIs based on the contrast (HC [self] – HC [other] > SD [self] – SD [other]) in the whole-brain analyses (Supporting Information: Table S3): left DMPFC (dACC/medial SFG) (peak: [−4, 40, 22], $k = 94$), left AI (peak: [−30, 18, −18], $k = 123$), and right AI (peak: [32, 16, −12], $k = 68$). Here, we report results of simple effects analyses comparisons between the SD and HC groups; results of another direction (the comparisons between the self and other conditions) are described in the Supporting Information: Part 2.

3.3.1 | Left DMPFC: reduced activation for self but a trend of enhanced activation for others in SD participants

For the beta value of left DMPFC activation, a three-way repeated-measures ANOVA on the factors of *group*, *recipient*, and *effort* revealed a significant interaction of *group* × *recipient* ($F_{(1,\ 61)} = 23.22$, $p < .001$, $\eta^2_p = 0.276$). A simple effects analysis indicated that, compared with the HC group, the SD group showed reduced left DMPFC activation when making effortful choices for self ($F_{(1,\ 61)} = 7.34$, $p = .009$, $\eta^2_p = 0.110$; 0.176 ± 0.346 vs. 1.534 ± 0.363); however, the pattern was reversed, that is, the SD group showed marginally significant increased left DMPFC activation when making effortful choices for others ($F_{(1,\ 61)} = 3.58$, $p = .060$, $\eta^2_p = 0.055$; 1.183 ± 0.333 vs. 0.271 ± 0.349). We produced three correlations between the beta values of three ROI activations and the TEPS-ANT score. After multiple tests correction using the FDR method, the left DMPFC activation in the "high-effort for self" condition positively correlated with anticipatory pleasure (TEPS-ANT) across all participants ($r = .309$, $p = .016$, corrected $p = .024$; Figure 3a).

3.3.2 | Left AI: reduced activation for self but enhanced activation for others in SD participants

For the beta value of left AI activation, a three-way repeated-measures ANOVA revealed a significant interaction effect of *group* × *recipient*

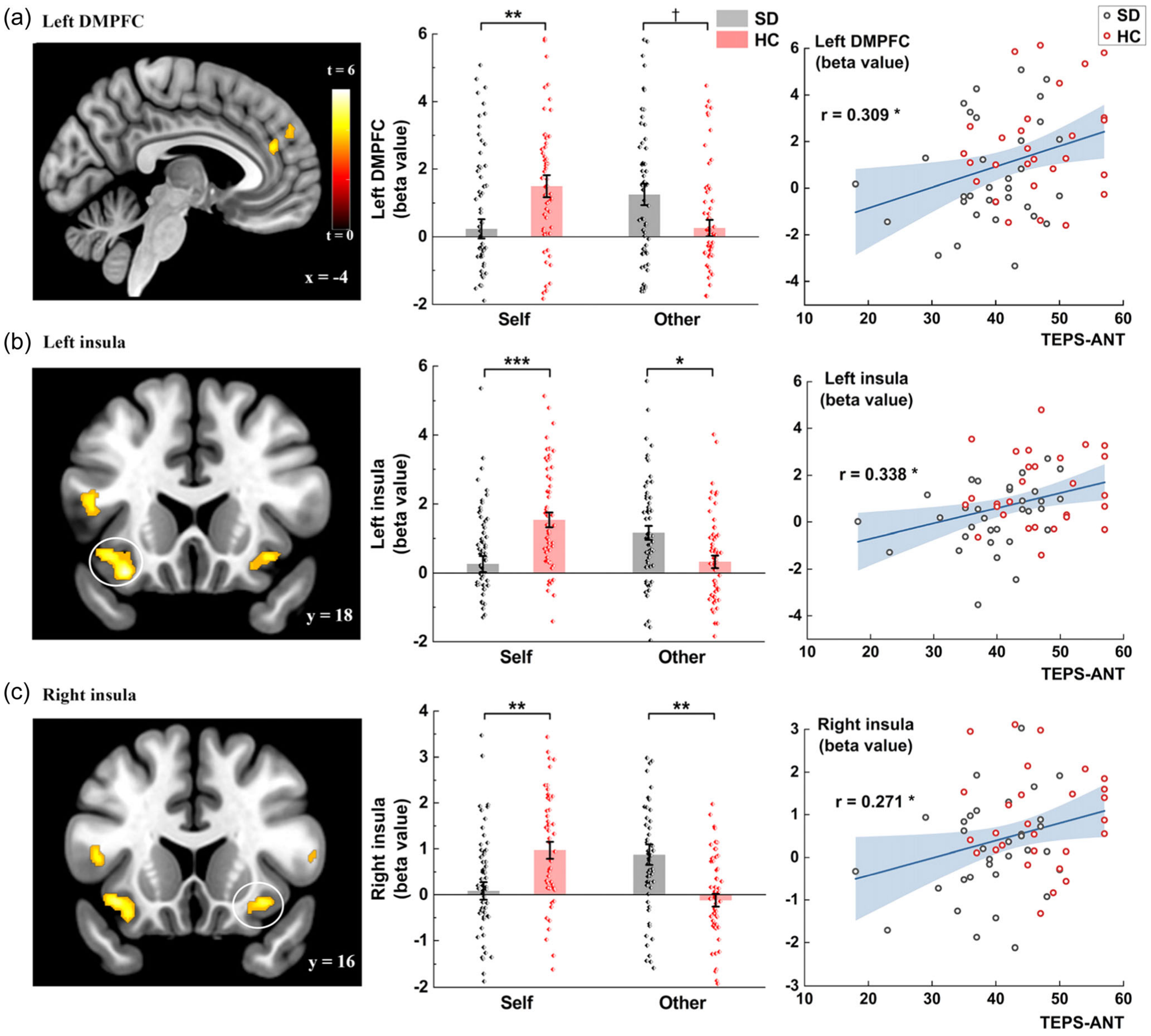

FIGURE 3 ROI results. Differences between the SD and HC groups as well as Pearson correlations between effortful decision-making activation in the "high-effort for self" condition and anticipatory pleasure (TEPS-ANT) for four greater activation cluster in *T*-contrast (HC [self] – HC [other] > SD [self] – SD [other]) from whole-brain analysis: (a) left dorsomedial prefrontal cortex (DMPFC), (b) left anterior insula, and (c) right anterior insula. Bars represent one standard error. Blue shaded areas represent regression lines with 95% confidence bands. All imaging maps are threshold at $p < .05$ with FDR correction. $^{\dagger}p < .1$, $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

($F_{(1,61)} = 29.42$, $p < .001$, $\eta^2_p = 0.325$). A simple effects analysis indicated that, compared with the HC group, the SD group showed reduced left AI activation when making effortful choices for self ($F_{(1,61)} = 9.70$, $p < .001$, $\eta^2_p = 0.183$; 0.211 ± 0.248 vs. 1.538 ± 0.260); however, the pattern was reversed, that is, the SD group showed increased left AI activation, when making effortful choices for others ($F_{(1,\ 61)} = 7.17$, $p = .010$, $\eta^2_p = 0.105$; 1.095 ± 0.197 vs. 0.332 ± 0.206). Across all participants, the neural activation of the left AI in the "high-effort for self" condition significantly positively correlated with anticipatory pleasure ($r = .338$, $p = .008$, corrected $p = .024$; Figure 3b).

3.3.3 | Right AI: reduced activation for self but enhanced activation for others in SD participants

For the beta value of right AI activation, a three-way repeated-measures ANOVA revealed a significant interaction effect of *group × recipient* ($F_{(1,\ 61)} = 25.76$, $p < .001$, $\eta^2_p = 0.297$). A simple effects analysis indicated that, compared with the HC group, the SD group showed reduced right AI activation when making effortful choices for self ($F_{(1,\ 61);} = 10.95$, $p = .002$, $\eta^2_p = 0.152$; −0.019 ± 0.201 vs. 0.983 ± 0.211); however, the pattern was reversed, that is, the SD group showed increased right AI activation, when making effortful choices for others ($F_{(1, 61)} = 9.27$, $p = .003$, $\eta^2_p = 0.132$; 0.777 ± 0.198 vs. −0.098 ± 0.208). Across all participants, the neural activation of the right AI in the "high-effort for self" condition positively correlated with anticipatory pleasure ($r = .271$, $p = .035$, corrected $p = .035$; Figure 3c).

3.4 | PPI analysis results

According to the whole-brain results, we performed PPI analysis to investigate whether the functional connectivity between the seed and other brain regions was modulated by effortful decision-making to reward self. With the left DMPFC or AI as the seed region, we did not observe any difference in functional connectivity for high [self] trials > low [self] trials.

However, with the right putamen as the seed region (with largest activation and cluster size in the contrast of high [self] > low [self]), we observed significant functional connectivity (whole-brain, FDR-corrected threshold $p < .05$) in two ROIs, that is, the left DMPFC (dACC/medial SFG) (peak: [−4, 30, 30], $k = 78$) and the left dorsolateral prefrontal cortex (DLPFC) (SFG) (peak: [−20, 8, 58], $k = 35$; Figure 4a and Supporting Information: Table S5). The complete results are reported in the Supporting Information: Part 3.

Among these two ROIs, we further explored group differences of functional connectivity with the right putamen. An independent samples *t*-test revealed a significant difference between groups for the left DLPFC ($t_{(61)} = -2.137$, $p = .037$), indicating that the SD group showed weaker functional connectivity between the right putamen and left DLPFC compared to the HC group (SD vs. HC = 0.289 ± 0.684 vs. 0.616 ± 0.508; Figure 4b). Across all participants, functional connectivity between the right putamen and left DLPFC was positively associated with the score of behavioral approach motivation (BAS-Drive; $r = .314$, $p = .014$; Figure 4c).

4 | DISCUSSION

This study employed fMRI to explore whether motivation of exerting effort in individuals with subthreshold depression would show altered neural patterns for rewarding self and others compared to HCs. Our results demonstrated that depressive individuals showed reduced left DMPFC and bilateral AI activations when making effortful choices for themselves, but enhanced activations in bilateral AI when making effortful choices for others. Also, they showed reduced functional connectivity between the right putamen and left DLPFC when making effortful choices for themselves. Moreover, these findings in brain activation and functional connectivity were positively associated with subjective ratings of motivational measures. Overall, our results indicate that individuals with SD have shown inversely motivational alteration of investing effort for self and others.

First, we found SD individuals exhibited hypoactivation in the DMPFC (covering dACC) and bilateral AI relative to HCs during effortful decision-making for self. To date, most effort studies have revealed that dACC/DMPFC encodes effort costs and trade-offs between effort and reward (Hauser et al., 2017; Hogan et al., 2019; Klein-Flügge et al., 2016). In line with these neuroimaging results, animal studies also revealed reduced willingness to make high-effort/high-reward choices with dACC lesions (Walton et al., 2009). Similarly, AI was thought to signal the net value discounted by effort costs (Arulpragasam et al., 2018). Thus, these brain areas play vital roles in driving motivation to decide whether the rewards are worth exerting the effort. In this study, SD participants had reduced ability

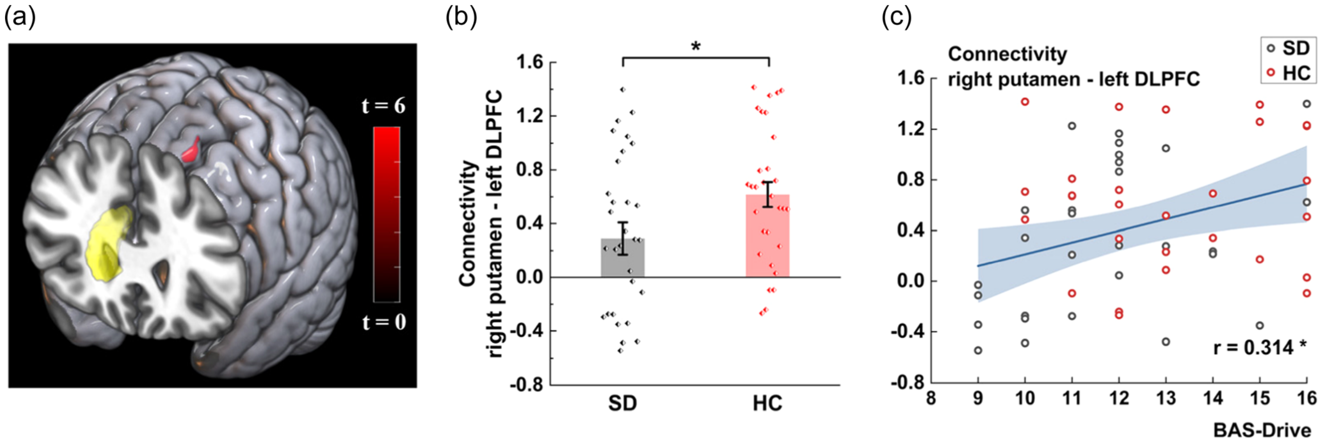

FIGURE 4 PPI results. (a) Functional connectivity between the right putamen (seed region, yellow) and the left dorsolateral prefrontal cortex (DLPFC, red). The image is threshold at $p < .05$ with FDR correction. (b) Functional connectivity differences between the right putamen and left DLPFC in the SD and HC groups. Bars represent one standard error. (c) Pearson's correlation analysis showed that the functional connectivity between the right putamen and left DLPFC was positively correlated with BAS-Drive scores. Blue shaded areas represent regression lines with 95% confidence bands. *$p < .05$.

to recruit the DMPFC to compare subjective value between decision options, as well as impaired engagement of the AI, to encode the net value when deciding whether to exert effort for self. Given that our amount of effort levels may not be sensitive to differentiate the behavioral decisions, which may result in the absence of group difference in effortful acts for self. Even so, our finding in neural response differences is somewhat in line with the proposal that depressed individuals may underestimate the potential benefits of obtaining rewards and fail to optimally integrate cost/benefit information (Park et al., 2017; Treadway & Zalda, 2011). Previous studies have demonstrated that these brain areas are dysfunctional in depressed individuals. For example, compared to healthy people, the MDD patients showed reduced activation in the dACC and insula during reward anticipation (Chase et al., 2013; Gotlib et al., 2010; Smoski et al., 2009). More relative to our work, Rzepa and McCabe (2019) focused on the effort phase of reward processing, and found reduced activity in the insula when anticipating rewards in adolescents with depressive symptoms compared with HCs.

We also found that SD individuals showed blunted functional connectivity between the right putamen and left DLPFC when making effortful choices for self. Previous studies have identified the putamen as the region representing effort costs (Burke et al., 2013; Kurniawan et al., 2013), and reduced effort-related putamen activity was associated with greater amotivation severity in depressed patients (Park et al., 2017). We found several brain areas (e.g., DMPFC, DLPFC) having connectivity with the right putamen (seed region), but only found a group difference in the left DLPFC. These findings are consistent with prior literature demonstrating that the DLPFC plays a key role in top-down control and facilitating goal-directed behaviors/action planning (Miller & Cohen, 2001; Zalla et al., 2001) and that impaired left DLPFC may lead to deficient motivation to generate and execute goal-directed action plans to obtain valued outcomes in depression (Barch et al., 2016). More relevant to our work, Soutschek and Tobler (2020) used transcranial direct current stimulation (tDCS) to disrupt the left DLPFC activation, resulting in reduced motivation to exert effort and slowed response during effort exertion. These authors thus concluded that the DLPFC can successfully deal with effort demands (Soutschek & Tobler, 2020). Moreover, studies focusing on depressive individuals often found hypoactivity in the left DLPFC (Grimm et al., 2008; Ironside et al., 2020) and impaired brain connectivity between the striatum and prefrontal cortex during reward anticipation (Manelis et al., 2016).

The most novel finding was that SD individuals were more likely to choose high effort options to benefit an unfamiliar other than the HC group, whereas, the HC group showed enhanced willingness to exert effort for self than others. This suggests that the SD group showed higher prosocial acts of exerting effort for others. Similarly, neuroimaging data found that depressive individuals showed hyperactivation in the bilateral AI and a trend of hyperactivation in the left DMPFC compared with HCs in the effort for other condition, which supports the hyper-altruism hypothesis revealing that MDD patients may exhibit increased altruistic behaviors due to their pathologically increased altruistic forms of guilt feelings (O'Connor et al., 2000, 2007, 2011). In line with this theory, individuals who worry too much about others' perspectives/benefits are more prone to depression (Akiskal, 1983; Alarcón & Forbes, 2017; von Zerssen et al., 1994). For instance, a previous study reported that depressive symptoms were more frequently found in prosocial people than in individualists during the Ultimatum Game (Tanaka et al., 2017) and that the amount of financial support provided to unfamiliar others than family members could predict the development of MDD (Fujiwara, 2009). Moreover, compared with HCs, Shao et al. (2015) found that women diagnosed with MDD showed more prosocial acts and blunted activation in the AI, putamen, and DLPFC in the contrast of selfish-prosocial during the Trust Game Task. Beyond these findings, our results provide novel evidence for higher motivation and prosocial acts of depressed individuals during effort-based decision-making.

Taken together, this study found that people with subthreshold depression showed altered neural responses in the prefrontal–striatal circuit during the effort anticipation stage; these neural responses were positively associated with self-report motivational measures. This finding is consistent with the evidence that depression is associated with impaired motivation and anticipatory anhedonia (Horne et al., 2021; Sherdell et al., 2012; Ubl et al., 2015). To further illustrate, a meta-analysis found that anticipatory anhedonia, that is, a diminished motivation/goal-directed behavior to pursue rewards (Berridge & Robinson, 1998; Treadway & Zalda, 2011), is highly dependent on prefrontal–striatal networks that guide behaviors to pursue rewards in the motivational/anticipatory stage (Der-Avakian & Markou, 2012; B. Zhang et al., 2016). Our findings in both the "self" and "other" conditions confirmed the importance of anticipatory alternation of effortful reward processing in subthreshold depression.

In addition to the above findings related to depression, this study provided evidence for different motivations for self and others across different levels of effort/reward. The behavior results revealed that HCs showed enhanced willingness to choose higher levels of effort-reward options in the self condition compared with the other condition, which is in line with the two behavior studies conducted by Lockwood et al. (2017) and Lockwood, Abdurahman, et al. (2021). Notably, this study employed fMRI and provided brain correlate findings showing greater brain activity in the left precuneus, ventromedial prefrontal cortex (VMPFC), and left posterior insula when participants decided whether to exert high effort for high rewards to benefit self (Supporting Information: Table S4). Accumulating evidence has consistently reported that the VMPFC encodes the net value integration of rewards discounted by effort costs across different cost/reward domains (Bartra et al., 2013; Levy & Glimcher, 2012; Lopez-Gamundi et al., 2021; Prevost et al., 2010). Meanwhile, the precuneus (a part of the posterior cingulate cortex) has been shown to encode subjective value (Bartra et al., 2013; Westbrook et al., 2019). More relevant to our work, a recent study revealed that the ventral insula prioritizes encoding subjective value when individuals choose to exert effort for themselves than for others (Lockwood, Wittmann, et al., 2021). Our work extended this study by highlighting the importance of the insula in deciding whether to exert high effort for high rewards to benefit self.

Our findings provide valuable implications for clinical practice. First, the finding that the blunted prefrontal–striatal circuit in subthreshold depression plays important roles in motivational alteration for self might contribute to refining the target regions of neuromodulation (e.g., transcranial magnetic stimulation [TMS], tDCS) to enhance patients' motivation for self. Previous tDCS/TMS studies improved the willingness to engage in both physical and cognitive effort for reward when targeting the frontopolar cortex (Soutschek et al., 2018) and changed the motivation for cognitive effort when targeting the DLPFC (Soutschek & Tobler, 2020). Beyond these studies, the present results suggest that the DMPFC and DLPFC may be ideal targets for TMS, or neurofeedback therapies, aimed at improving depressed patients' motivation to engage in various enjoyable activities. Second, SD individuals showed inversely motivational alteration for themselves and for others when exerting effort to obtain rewards, which suggests that clinical treatment should not confuse the two conditions of benefiting self and others, that is, different patterns of motivation alteration should be clarified and thus different preventions and treatment strategies should be developed.

Despite these invaluable findings, one limitation of this study was that our sample included those with mild depressive state; thus, whether the conclusions drawn here can be generalizable to the wider population, especially for clinical depression, remains to be confirmed. Therefore, future studies should address this limitation when expanding this study's findings.

5 | CONCLUSION

The present study revealed that people with the mild depressive state showed altered motivation when exerting effort for rewards in different interpersonal contexts, with less neural response for themselves, but higher motivation acts and brain activations for others. These motivational alterations during effort-based decision-making are subserved by the altered prefrontal–striatal circuit, including the left DMPFC, AI, left DLPFC, and putamen. Our findings highlight the anticipatory anhedonia and hyper-altruism in subthreshold depression. Moreover, our findings suggest that the DMPFC and DLPFC may be therapeutic targets for TMS or neurofeedback in depression. Thus, our findings have revealed differences between the two situations (self vs. other) and have emphasized that treatment strategies should not confuse these situations when addressing motivation for the self and others.

AUTHOR CONTRIBUTIONS

Rong Bi and Dandan Zhang designed research. Rong Bi, Wanxin Dong, and Zixin Zheng performed the experiment and collected data. Rong Bi analyzed the data. Rong Bi and Dandan Zhang wrote the manuscript. Sijin Li revised the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code of this study would be available upon reasonable request and with approval of the School of Psychology, Shenzhen University. More information on making this request can be obtained from the corresponding author, D. Zhang (zhangdd05@gmail.com).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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