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RESEARCH ARTICLE

The neuroanatomical basis of the Gambler's fallacy: A univariate and multivariate morphometric study

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Abstract

Human decision-making can be irrational, as in the case of the gambler's fallacy (GF). Converging evidence from behavioral and functional neuroimaging studies has suggested that a hyperactive cognitive system and a hypo-active affective system contribute to the false world model that generates the GF. However, the neuroanatomical basis underlying the GF remains unclear. The current study addressed this issue by collecting high-resolution magnetic resonance anatomical images from a large sample of 350 healthy Chinese adults. Univariate voxel-based morphometry (VBM) analysis suggested that the gray matter volume (GMV) in the anterior cingulate cortex (ACC) and medial temporal lobe (MTL) (two regions of the cognitive system) showed negative correlations with the degree of GF, while the GMV in the striatum and orbitofrontal cortex (OFC; two regions of the affective system) showed positive correlations. Further multivariate VBM analysis showed that the GMV in these regions could potentially predict the degree of GF. Moreover, a mediation analysis suggested that the GMV in MTL, ACC, and OFC mediated the relationships between the cognitive abilities or affective decision-making performance and the GF. Results of our study help us to understand the potential neural bases of the cognitive system's constructive role and the affective system's destructive role in decision making.

KEYWORDS
decision making, Gambler's fallacy, mediation, multivariate pattern analysis, voxel-based morphometry

1 | INTRODUCTION

It has been widely demonstrated that humans often make suboptimal decisions when dealing with random events. One suboptimal decision-making strategy is the "gambler's fallacy" (GF), characterized by a tendency to believe that the occurrence of a certain random event is less likely after a series of the same event. Several theories have been proposed to explain the GF: The law of small numbers (Tversky & Kahneman, 1971), the causal model (Moldoveanu & Langer, 2002), Gestalt theory (Militana, Wolfson, & Cleaveland, 2010), and Urn model (Rabin, 2002). Recent studies have suggested that the GF is a cognitive bias resulting from wrong beliefs about the specific generating mechanisms, such as the tendency to regard a sample as representative of the population distribution (i.e., the law of small numbers). Computational models demonstrated that a rational mind guided by a false "world model" could produce such suboptimal decisions (Green, Benson, Kersten, & Schrater, 2010).

One recent study (Xue et al., 2012) provided evidence that the GF might be due to an imbalance between the cognitive and affective systems. Specifically, Xue, He, et al. (2012) found that the use of the

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GF strategy was negatively correlated with the affective decision-making capacities (the affective system), and positively correlated with general intelligence and executive functioning (the cognitive system). Furthermore, functional neuroimaging and lesion studies have confirmed the involvement of both cognitive and affective systems in GF and GF-like maladaptive decisions. For example, in their study, using transcranial direct current stimulation (tDCS), Xue, Juan, Chang, Lu, and Dong (2012) found that anodal tDCS over the left lateral prefrontal cortex (LPFC) increased the GF. Other studies have shown that patients with damages in the ventromedial prefrontal cortex (VMPFC)/orbitofrontal cortex (OFC) exhibit behavior patterns that resemble the GF (Bechara, Damasio, & Damasio, 2000; Bechara, Damasio, Tranel, & Damasio, 1997; Shiv, Loewenstein, Bechara, Damasio, & Damasio, 2005). These patients continued to choose the disadvantageous decks in the Iowa Gambling Task (IGT) even after they suffered heavy losses, presumably because they believed their luck was going to change. In sum, both cognitive (i.e., the LPFC) and affective systems (the VMPFC/OFC) seem to be related to the GF.

Based on the evidence reviewed above, we proposed that the GF is a possible result of hyperfunction in the cognitive system and hypofunction in the affective system (Xue, He, et al., 2012). We argue that the win-stay/lose-shift (WSLS) strategy is the prepotent strategy because of a reinforcement learning mechanism (Barraclough, Conroy, & Lee, 2004). In contrast, the GF uses the opposite win-shift/lose-stay strategy based on a false world model. One possible explanation is that it takes more cognitive control capacity for individuals to implement the false world model and use the GF strategy in place of the prepotent WSLS response. Participants with strong affective decision-making capacities, on the other hand, can resist nonoptimal and nonadaptive decisions like the GF. Thus far, no study has provided neuroanatomical evidence for the relationship between the GF and cognitive/affective systems.

Cerebral gray matter volume (GMV) has been widely associated with function/behavioral performance in samples with neuropathology and in healthy individuals. For instance, researchers have reported negative correlations between memory performance and the GMV of the medial temporal lobe in healthy young adults (Chantôme et al., 1999; Foster et al., 1999). Foster et al. (1999) further suggested that "insufficient pruning of the hippocampus during childhood and adolescence (following adequate growth) may lead to reduced mnemonic efficiency" in healthy individuals. Structural changes such as alterations in GMV are also likely to underlie dysfunctions in the neural system, because "[s]tructure invariably informs and constrains biological function" (Honey, Thivierge, & Sporns, 2010). One way to examine such structural changes is to use voxel-based morphometry (VBM), an automated, unbiased whole-brain analysis involving voxel-wise comparisons of the probabilities of the presence of gray or white brain matter (Ashburner, Friston, Price, & Mechelli, 2005).

In the present study, we used both univariate and multivariate VBM to examine the correlation between the GF and brain morphometry underlying the cognitive and affective systems in a large sample of Chinese college students. Compared with univariate analysis, multivariate pattern analysis has been shown to have greater sensitivity and to be more predictive of behavioral performance (He et al., 2013; Jimura & Poldrack, 2012). In addition, mediation analysis was used to find the most relevant brain regions mediating the relationship between the GF and cognitive/affective systems. Consistent with the previous studies demonstrating that the GF results from the cognitive system's hyperfunction and the affective system's hypofunction, we hypothesized that the GMV in brain regions for the cognitive system (including LPFC) and the affective system (including VMPGC/OFC) would be correlated with the degree of GF.

2 | MATERIALS AND METHODS

2.1 | Participants

A total of 350 (194 females; mean age = 19.7 years old, SD = 1.02; mean number of years of education = 16.3, SD = 0.96) Chinese undergraduate students were recruited to participate in this study. They were selected from a large-scale gene-brain-behavior project with complete data for (a) the GF task, (b) high-resolution structural MRI scan, and (c) two cognitive tasks and one affective task. All subjects had normal or corrected-to-normal vision and were free of neurological or psychiatric history. Informed written consents approved by the Institutional Review Board of Beijing Normal University were obtained from all participants after they were fully informed of the purposes and procedures of the current study.

2.2 | The Gambler's fallacy task

The Card Guessing Task [adapted from Xue, Juan, et al., 2012] was used to measure the degree of GF. Subjects were asked to guess the computer's choice of cards (either red or black). Detailed information regarding this task was described in Xue, Juan, et al. (2012). Briefly, as shown in Figure 1, a trial began with two cards (red and black) presented on the left and right sides of the screen, respectively. The positions of the two cards were randomly assigned. The computer (C1) chose one card in 1 s. The subject (P2) was then asked to guess which one was chosen by the computer by pressing the corresponding button within 2 s. Then, we showed the feedback (choices by both the computer and the subject) for 1 s. The subject won one Yuan (RMB) for each correct guess and lost one Yuan for each incorrect guess. Subjects were told explicitly that the computer chose the cards randomly (i.e., the probability of choosing each card was 50%). To motivate the participants, they were told that they would be paid the exact amount they won after the experiment. To reduce the working memory load, the computer's last five choices were presented on the top of the screen. The whole procedure consisted of two 63-trial sessions.

Following the previous study (Xue, Juan, et al., 2012), we designed the computer's card choices based on a predetermined, canonical random sequence generated by a Bernoulli process with the following characteristics: (a) the numbers of red and black cards chosen by the computer were equal, (b) half of the trials involved switching, and (c) the streak length had an exponential distribution. The procedure guaranteed that at any streak length, the probability that a streak will continue or break is always 50%. The optimal strategy for individuals is to choose the red or black card randomly.

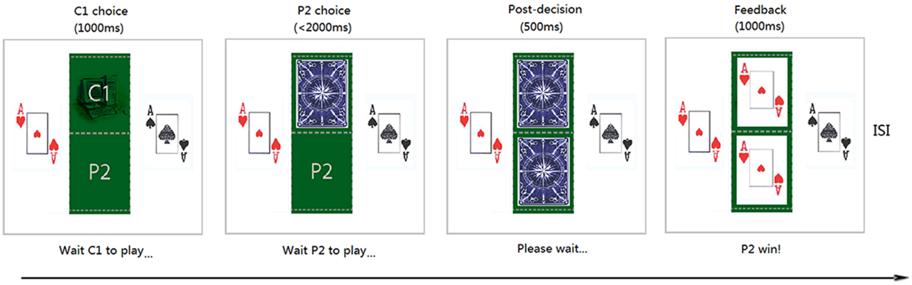

FIGURE 1 Experimental paradigm. Subjects were asked to guess the computer's choice (black or red card). Not shown here, the computer's most recent five choices were shown on the top of the computer screen to reduce working memory load [Color figure can be viewed at wileyonlinelibrary.com]

We calculated the percentage of trials using the GF strategy based on the length of streaks (1–6) that the computer made. For the remaining trials, subjects used the WSLS strategy: that is, wsls = 1-gf (the lowercase letters represent the percentages of trials using these two strategies). Lagged logistic regression analysis was used to examine the effect of outcome feedback (gain vs. loss), streak length (1–6), the interaction of the above two factors, and the cumulative probability of the current card on subjects' next strategy (GF vs. WSLS). The accuracy of the model was determined using the following equation:

$$y = \frac{1}{1 + e^{-f(x)}}$$

where *f(x)* represents the regression function and *y* is the model prediction.

2.3 | Cognitive tasks

The cognitive system was measured by two tasks, the 2-back working memory task (WMT) and the Stroop task. Detailed information on these two tasks can be found in our previous work (Xue, He, et al., 2012). Briefly, the 2-back WMT consisted of three sessions: semantic, phonological, and morphological judgment. The averaged accuracy of three sessions was used as the index of working memory performance. The classic Color-Word Stroop task was used to measure executive function. Subjects were asked to respond as quickly as possible to the printed color (not the meaning of the color word) using four buttons. The reaction time difference between the incongruent and congruent trials was taken as the measure of executive function.

2.4 | Affective task

The Iowa Gambling Task (IGT) was used to measure the affective system. A detailed description of the IGT used in this study can be found in our previous works (He et al., 2010; He et al., 2012; He et al., 2014; He et al., 2015; Koritzky et al., 2013). Briefly, participants were asked to choose from four decks of cards. After each selection, they were told how much money they had won or lost. Two decks (A and B) provided higher rewards but also higher punishments, whereas the other two decks (C and D) provided smaller rewards but also smaller punishments. The IGT scores (the number of selections from good decks minus the number of selections from bad decks) served as an index of the affective system.

2.5 | MRI data acquisition and preprocessing

Structural MRI data were acquired using a 3.0 T Siemens MRI scanner in the MRI Center at Beijing Normal University. A T1-weighted, 3D, gradient-echo pulse-sequence (MPRAGE) was used for the anatomical imaging data acquisition. The following parameters were adopted: repetition/echo times, 2,530 ms/3.39 ms; flip angel, 10°; field of view, 256 × 256 mm; matrix, 256 × 256. About 208 sagittal slices were acquired with 1 mm thickness, and final resolution was 1 × 1 × 1 mm.

MRI structural data were processed with VBM protocol performed in FSL (Good et al., 2001). Brain extraction and tissue-type segmentation were first carried out on the structural images, and the resulting images were then aligned to MNI152 standard space. The spatially normalized images were averaged to produce a study-specific GM template, to which the native GM images were both linearly and nonlinearly re-registered. The registered partial volume images were then modulated by dividing them by Jacobian of the warp field to correct for local expansion or contraction. The modulated segmented images, which were representative of the GMV, were then smoothed with an isotropic Gaussian kernel with a sigma of 3 mm.

2.6 | Univariate VBM analysis

General linear models were fitted to correlate the GMV with the degree of the GF. Nonparametric permutation methods (Randomize v2.1) were used for inference on statistic maps (Winkler, Ridgway, Webster, Smith, & Nichols, 2014). The null distribution at each voxel was constructed using 10,000 random permutations of the data to ensure that observed results were not due to chance. Because there were hundreds of voxels in the areas of interest, we corrected for multiple comparisons using threshold-free cluster enhancement (TFCE) with $p < .05$ across the whole brain.

2.7 | Multivariate VBM analysis

Epsilon-insensitive support vector regression (SVR) with a linear kernel was conducted on the preprocessed data to predict the degree of the GF through PyMVPA (Multivariate Pattern Analysis in Python; http://www.pymvpa.org/) (Hanke et al., 2009). The measure of prediction accuracy in the neighborhood of each voxel was implemented using the searchlight procedure with a three-voxel radius (Kriegeskorte, Goebel, & Bandettini, 2006). In accordance with previous studies (He et al., 2013; Jimura & Poldrack, 2012), we set the ε

parameter in the SVR as 0.01. Similar to previous reports (He et al., 2013), we used the 10-fold leave-one-out cross-validation to estimate the degree of the GF for each subject. The 350 subjects were divided into 10 groups of 35 people each, with matched means and standard deviations of behavioral performance. In each cross-validation, we selected the data of nine groups (315 subjects) to train an SVR model, which was then used to analyze the imaging data of the excluded group to predict the degree of the GF. We calculated the accuracy of SVR prediction for each voxel, which was defined as the Pearson's correlation coefficient between predicted and actual scores of the subjects' performance. The randomization test was then conducted to estimate the probability distribution of classifier accuracy under the null hypothesis (i.e., the degree of the GF was not correlated with GMV). The degree of the GF was first randomly shuffled across subjects for each analysis. The shuffle was performed within each group to guarantee that each group's gender ratio and distribution of behavior performance were not affected. The data were permuted and analyzed 1,000 times to generate a distribution of the association coefficients (classifier accuracy of prediction). Due to the extremely heavy computation requirements (>24,000 hr) for a region-of-interest (ROI) searchlight permutation test, we did it only on each cluster with a prediction accuracy >0.138 (approximate to an uncorrected threshold of $p = .05$). The prediction accuracies in these regions were all above 95th percentile of the permutation. Based on the results of multivoxel pattern analysis (MVPA) with a prediction accuracy >0.138 (obtained by the permutation test of false-positive rate in MVPA [$p < .05$]), we could identify the brain regions whose GMV could predict the degree of GF.

3 | RESULTS

3.1 | Behavioral results

Consistent with previous research (Ayton & Fischer, 2004; Burns & Corpus, 2004; Tversky & Kahneman, 1971), the degree of the GF increased with streak length [F (5,1,745) = 188.66, $p < .001$, Figure 2a]. For example, the percentage of trials using the GF strategy was lower (41.72%) following short streaks (≤3) than that following long streaks (≥4, 59.49%; $t = 18.372$, $p < .001$, Figure 2b). These results suggested that the subjects were more likely to break the random sequence after long streaks in the computer's choices. There were substantial individual differences in the degree of the GF following both short and long streaks (Figure 2c, d). No correlation was found between the degree of the GF strategy and gender or age.

For a predetermined sequence of given lengths, the local cumulative probability of a certain card would increase under long streaks (≥4) but decrease when the sequence became even longer. In that case, tracking the cumulative probability and using it to guide decisions would be considered rational. Because a reliance on either the streak length or the cumulative probability would both result in the same decision, it is necessary to distinguish between them. In the present study, we carefully selected sequences in which there was little

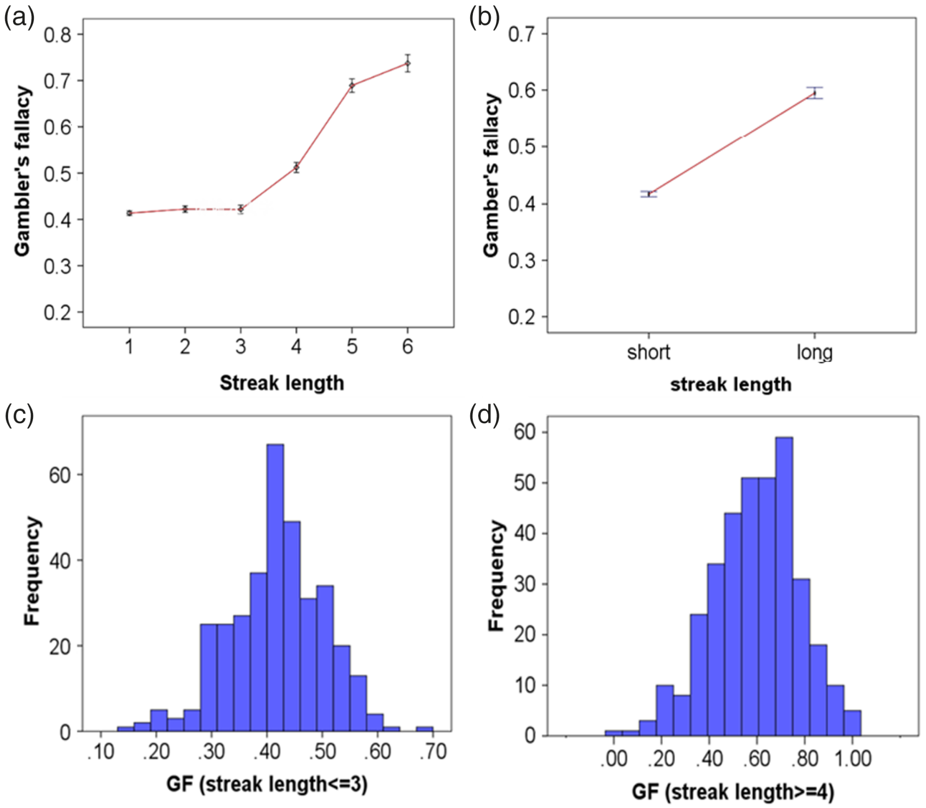

FIGURE 2 (a) Shows the mean percentage of trials using the GF strategy following different streak lengths, with (b) showing the average results for short streaks (≤3) and long streaks (≥4). (c and d) show the histograms of individual differences in the degree of the GF following short streaks (≤3) and long streaks (≥4), respectively [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Summary of cognitive and affective measures (N = 350)

Task	Measure	Mean	*SD*	Correlation with GF
WMT	Accuracy (%)	86.39	6.72	$r = .217, p < .001$
Stroop	RT(ms): Incog–Cong	138.63	71.65	$r = .196, p < .001$
IGT	IGT score (C + D–A–B)	6.28	12.36	$r = –.225, p < .001$

GF = Gambler's fallacy; WMT = working memory task; Incong = incongruent; Cong = congruent; IGT = Iowa gambling task.

TABLE 2 Brain regions showing significant positive correlations between GMV and the degree of the GF in univariate analysis

Brain regions	L/R	Voxels	TFCE corrected *p*	MNI *x*	MNI *y*	MNI *z*
Striatum	R	198	.0260	16	6	−2
Striatum	L	183	.0320	−26	10	4
OFC	L	106	.0270	−12	20	−28

OFC = orbitofrontal cortex.

correlation between the streak length and the cumulative probability (r = .12, p = .18). It would be obvious that subjects used the GF strategy if they consistently deviated from the computer's last choice following longer streaks even after the effect of cumulative probability was controlled. In the lagged logistic regression analysis that we used to examine this issue, the streak length (1–6), outcome feedback [win (1) vs. lose (–1)], the interaction of the above two factors, and the cumulative probability of the current card were independent variables, and individuals' next strategy [deviated from (1) vs. following (0) the computer's current choice] was the dependent variable. The results showed a significant effect of streak length on subjects' decisions (β = 0.1981, t = 14.789, p < .001), indicating that subjects were more likely to deviate from the computer's choice (GF strategy) when the streak got longer. There was also a significant effect of outcome feedback on subjects' decisions (β = –0.1185, t = –4.38, p < .001), with subjects tending to stick with the computer's last choice if they guessed it correctly. The interactions between the above two variables and cumulative probability were also significant (β = 0.1172, t = –9.459, p < .001; β = –1.1556, t = –21.355, p < .001). The mean accuracy of the prediction of subjects' choices was 63.94% by applying this model to each subject [t(349) = 39.737, p < .001].

Further analysis of the results showed that the response times were affected by the last outcome [longer if they lost: t(349) = 5.7, p < .001], subjects' current choices [longer if they switched: t (349) = 2.96, p < .01], subjects' current strategy [longer if they used the GF strategy: t (349) = 8.66, p < .001], and streak length [shorter if streaks got longer, F(5,1,745) = 25.06, p < .001].

Table 1 shows the descriptive statistics of the cognitive and affective measures as well as their correlations with the degree of the GF. Consistent with our previous report, we found significant positive correlations between cognitive functions and the degree of the GF, but a significant negative correlation between affective functions and the degree of the GF (Table 1).

3.2 | Univariate VBM results

Previous studies (Ayton & Fischer, 2004; Johnson, Tellis, & Macinnis, 2005; Xue, Juan, et al., 2012) have showed that subjects preferred to use the WSLS strategy following short streaks (≤3), and they tended to switch to the GF strategy when streaks got longer (usually starting with a streak length of 4), indicating the GF strategy became dominant in the long streak condition. Other studies have also used the trial following a run of four of the same event as the critical trial to measure GF behavior (Mossbridge, Roney, & Suzuki, 2017). We thus used the GF strategy rate only under the long streaks (≥4) as a measure of individuals' GF strategy tendency. Therefore, single-voxel analysis was conducted using the degree of the GF following long streaks (≥4) as the parameter of the FSL-VBM analysis to identify the brain regions whose GMV was correlated with the degree of the GF. As summarized in Table 2 and Figure 3, results suggested that the degree of the GF was positively correlated with the GMV mainly in the striatum (putamen) and OFC. The binary masks were first derived from the resulting regions, and the GMV of these regions were then extracted using *fslmeants* and were applied to the subsequent ROI analyses. ROI analysis suggested that these effects were still significant even after controlling for the effect of gender and age [right striatum (r = .136, p = .012 < .05), left striatum (r = .144, p = .008 < .05), and OFC (r = .170, p = .02 < .05)]. On the other hand, as presented in Table 3 and Figure 4, the degree of the GF was inversely correlated with GMV in the anterior cingulate cortex (ACC), frontal pole (FP), and bilateral medial temporal lobe (MTL). ROI analysis suggested that three regions were still significant even after controlling for the effect

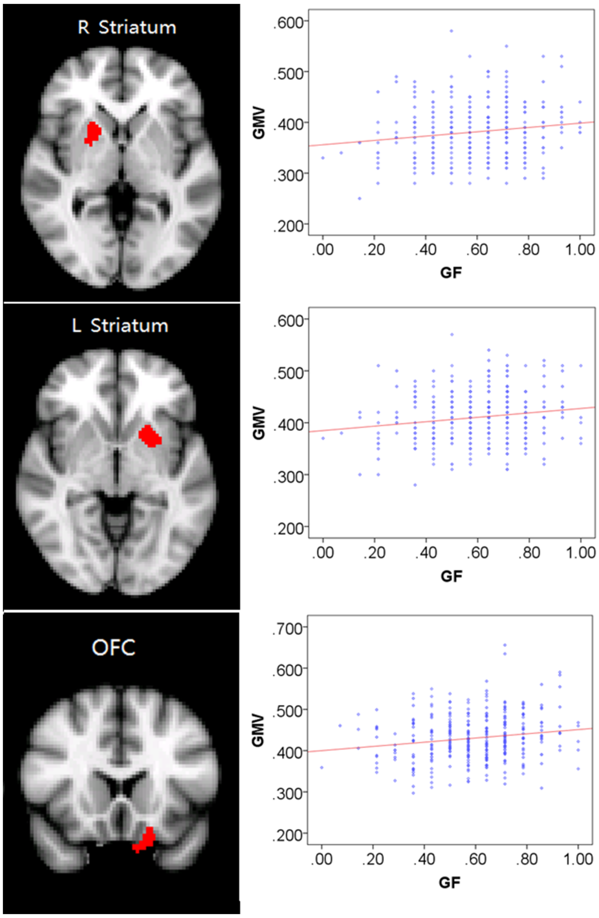

FIGURE 3 GMVs of the right and left striatum as well as OFC were positively correlated with the degree of the GF in univariate analysis [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Brain regions showing significant negative correlations between GMV and the degree of the GF in univariate analysis

Brain regions	L/R	Voxels	TFCE corrected *p*	MNI *x*	MNI *y*	MNI *z*
TL/MTL	L	6,444	<.0000	−40	−16	−42
TL/MTL	R	3,643	.0010	50	20	−32
ACC	R	592	.0100	14	6	40
FP	L	433	.0200	−14	54	6
IFG	L	402	.0090	−62	12	6

TL = temporal lobe; MTL = medial temporal lobe; ACC = anterior cingulate cortex; FP = frontal pole; IFG = inferior frontal gyrus.

of gender and age [ACC ($r = -.161$, $p = .003 < .05$), FP ($r = -.178$, $p = .001 < .05$), MTL ($r = -0.129$, $p = .017 < .05$)].

3.3 | Multivariate VBM results

Using multi-variable analyses as implemented in PyMVPA, we identified the brain regions whose GMV could predict the degree of the GF following long streaks (≥4). Consistent with univariate analysis, significant regions included left MTL, left OFC, bilateral striatum, and bilateral ACC (see Table 4 and Figure 5 for details). Moreover, the mean GMV for each significant ROI was extracted and then used for the correlation analysis with the degree of GF. The degree of the GF had negative correlations with the GMV in ACC ($r = -.143$, $p = .008 < .05$) and MTL ($r = -.157$, $p = .003 < .05$), but positive correlations with the GMV in OFC ($r = .176$, $p = .001 < .05$) and striatum ($r = .168$, $p = .002 < .05$), after controlling for gender and age.

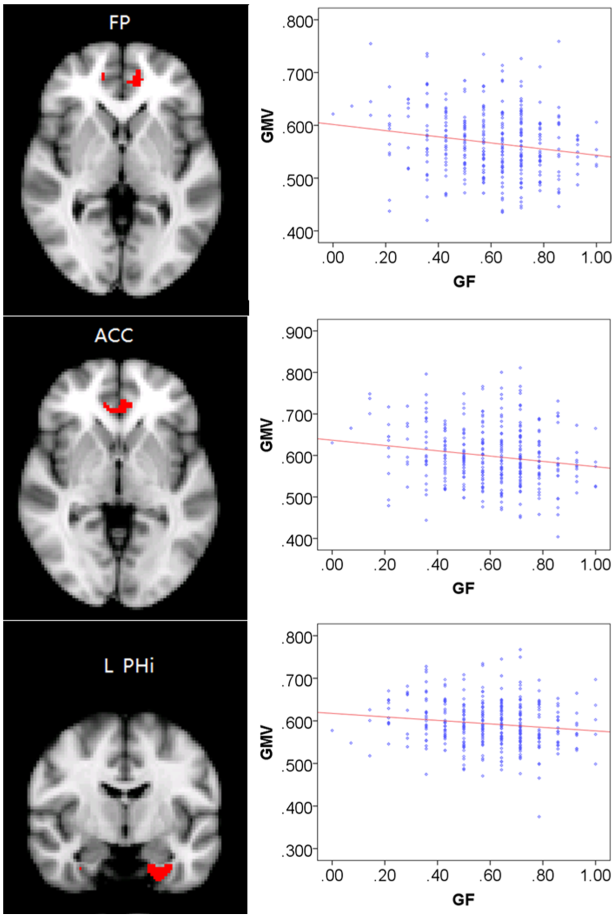

FIGURE 4 GMVs of FP, ACC, and left MTL were negatively correlated with the degree of the GF in univariate analysis [Color figure can be viewed at wileyonlinelibrary.com]

3.4 | Mediation analysis results

Using Hayes's (2013) PROCESS macro implemented in SPSS, mediation analysis was conducted to explore whether the GMV identified in the univariate and multivariate analyses mediated the links between cognitive/affective behaviors and the degree of the GF. A bootstrapping procedure (with 5,000 bootstrap samples) to estimate 95% confidence intervals (CI) was used. If the 95% CI for the product of indirect paths did not include zero, there was evidence for a significant indirect effect (Hayes, 2009; Preacher and Hayes, 2008). Bonferroni correction was applied to correct for family-wise errors.

As shown in Figure 6, mediation analysis suggested that the following models were significant: GMV in MTL mediated the relationship between working memory and the degree of the GF (Figure 6a), GMV in ACC mediated the relationship between executive function and the degree of the GF (Figure 6b), GMV in OFC mediated the relationship between affective decision making and the degree of the GF (Figure 6c). These results suggested that the use of GF strategy was influenced by a strong cognitive system (working memory and executive function) mediated by GMV in ACC and MTL, and by a weak affective system (affective decision making) mediated by OFC.

4 | DISCUSSION

The present study aimed to investigate the underlying neuroanatomical basis of the GF, and to disentangle specific roles of the cognitive and affective systems. Both univariate and multivariate VBM analyses implicated brain regions in the cognitive system (e.g., ACC, MTL) and the affective system (e.g., striatum, OFC) in the GF. Mediation analysis further suggested the GMV in the MTL, ACC, and OFC mediated the relationships between cognitive abilities or affective decision-making performance and the degree of the GF.

The GF is generally regarded as a cognitive bias or a wrong belief that arises from a false perception of random events (e.g., the small number law) (Tversky & Kahneman, 1971). Because the opposite strategy (WSLS) is guided by the free-model reinforcement learning and hence of relatively high prepotency, it may require a high level of cognitive control to use the GF strategy (Xue, He, et al., 2012). As a result, individuals with stronger executive function are more likely to use the GF strategy, which was clearly revealed in our results and

TABLE 4 Brain regions showing significant correlations between GMV and the degree of the GF in MVPA analysis

Brain regions	L/R	Voxels	Prediction accuracy	MNI *x*	MNI *y*	MNI *z*
MTL	L	1,366	0.219	−34	−18	−38
Striatum/OFC	L	367	0.177	−16	14	−12
Striatum	R	167	0.182	8	2	0
ACC	L and R	145	0.160	−4	2	42

MTL = medial temporal lobe; OFC = orbitofrontal cortex; CC = cingulate cortex.

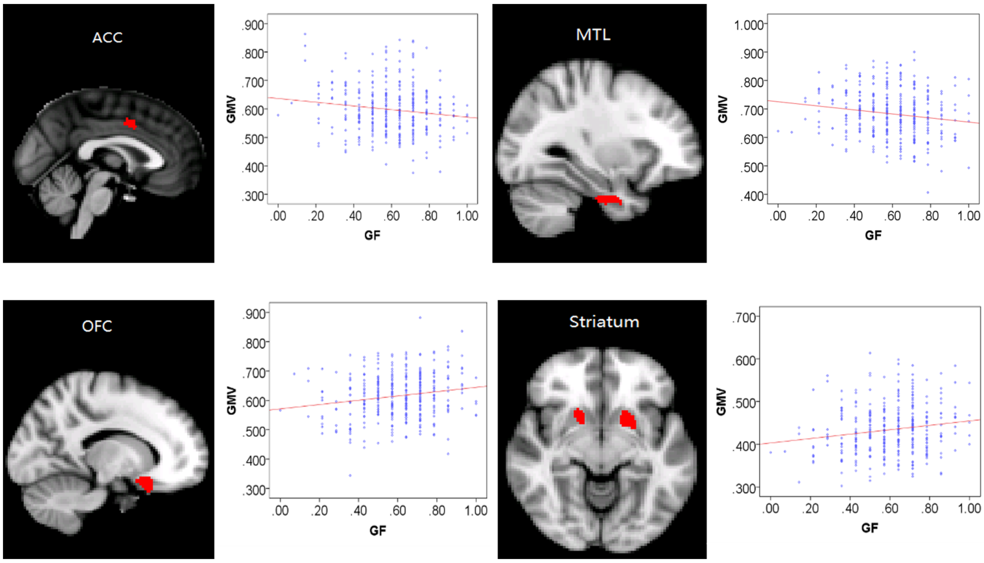

FIGURE 5 The GMV in ACC and MTL were positive predictors of the degree of the GF in the multivariate analysis, whereas the GMV in OFC and striatum were negative predictors [Color figure can be viewed at wileyonlinelibrary.com]

consistent with our previous work. More importantly, we uncovered its underlying neuroanatomical mechanism for the first time. The GMV in ACC was negatively correlated with the degree of the GF and mediated the relationship between executive function and the degree of GF. This finding is in line with the crucial role of the ACC in monitoring and resolving response conflicts (Braver, Barch, Gray, Molfese, & Snyder, 2001) generated by, in this case, the implementation of the GF strategy while holding the prepotent WSLS response.

There were also negative correlations between the GMV in MTL and FP and the degree of the GF, and the GMV in MTL mediated the relationship between working memory and the degree of the GF. These results are in accordance with previous studies suggesting that MTL serves as one of the critical components of the memory system (e.g., Squire & Zolamorgan, 1991) and that MTL represents stimuli held in working memory (Kornblith, Quian Quiroga, Koch, Fried, & Mormann, 2017). MTL may be involved in the retrieval of the last few outcome feedbacks, which helps to promote the use of GF strategy. On the other hand, it was suggested previously that activation in the FP (and also in the PCC) was stronger before the use of WSLS strategy than before the use of the GF strategy on the next trial (Xue, Juan, et al., 2012). The primary contributions of the FP to decision making are believed to be tracking the reward probability of the unchosen option (Boorman, Behrens, & Rushworth, 2011) and to compute the value of alternative options especially when a loss is experienced (Xue, Juan, et al., 2012). Our results regarding the FP were inconsistent between the univariate (significant) and multivariate analyses (not significant), which suggested that the FP may be not sensitive to the implementation of the GF strategy.

In contrast to the hyperfunction of the cognitive system in the use of GF strategy, the affective system showed hypofunction. The GMV in both OFC and striatum were positively correlated with the degree of the GF, and the GMV in OFC mediated the relationship between affective decision making and the degree of the GF. It has been well-documented that OFC/vmPFC has a major influence on affective decision making. For example, Xue et al. (2009) found that the vmPFC responded sensitively to the magnitude of the experienced gain or loss. Another study found that OFC/vmPFC activation was associated with fewer irrational decisions enabled by the frame effect (De Martino, Kumaran, Seymour, & Dolan, 2006). Furthermore, patients with OFC/vmPFC damage could not develop affective markers (e.g., the anticipatory skin conductance responses) to a disadvantageous choice based on prior gain or loss (Bechara et al., 1997), which resembled the behavioral pattern of the GF. The ventral striatum is widely recognized as playing a major role in reinforcement

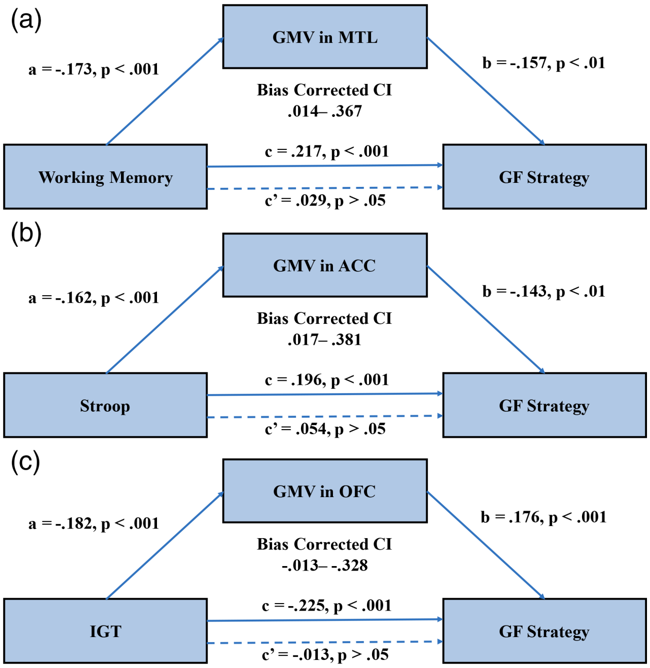

FIGURE 6 Mediation analysis results. (a) GMV in MTL mediated the relationship between working memory and GF, (b) GMV in ACC mediated the relationship between executive function and GF, and (c) GMV in OFC mediated the relationship between affective decision making and GF [Color figure can be viewed at wileyonlinelibrary.com]

learning (Rutledge, Dean, Caplin, & Glimcher, 2010) because this region is responsible for integrating signals of dopaminergic reward prediction errors (RPEs, the difference between experienced and predicted rewards) and hence facilitating learning (Collins & Frank, 2014). A dysfunction in the ventral striatum would impair learning and result in maladaptive decision making like the GF.

However, we remain cautious about the interpretation of the results, as findings from some GF studies contradict our results. For example, Clark, Studer, Bruss, Tranel, and Bechara (2014) found that lesions to the insula, which theoretically belongs to the affective system, abolishes the GF, while there is no involvement of vmPFC and amygdala in the GF. Nevertheless, these results are also in conflict with previous studies. In addition to vmPFC/OFC, which was previously found to be involved in nonadaptive decision making (Bechara et al., 1997; Bechara & Damasio, 2000) and pathological gambling (Lawrence, Luty, Bogdan, Sahakian, & Clark, 2009; Reuter et al., 2005),the insula has been found to play a role in decision making. One study found that patients with insula damage performed poorly on the IGT (Bar-On, Tranel, Denburg, & Bechara, 2003). Using the Cambridge Gamble Task, Clark et al. (2008) also found that patients with insula damage failed to adjust their bets by the odds of winning and eventually lost more money. Although the contradiction in these results are likely to be caused by different measurements and/or the heterogeneous lesions to the same brain regions, further studies are needed to clarify the consistencies.

Finally, we need to comment on the direction of our correlations between GMV and behavioral performance. We found that larger GMV was linked to poorer functions of the cognitive and affective systems. Such findings are not unusual. For example, increased cortical thickness in large brain regions was observed in children with prenatal alcohol exposure compared to healthy controls (Sowell et al., 2008). The cortical gray matter thickness was found to decrease with age between the ages of 5–20 years (Gogtay et al., 2004). Heflin et al. (2011) found that bilateral ACC atrophy actually predicted better Stroop performance.

Several limitations of this study must be noted. First, our interpretation of the results was based on the traditional theory of cognitive–affective dual system, but it should be acknowledged that this may not be the only reasonable explanation. On the one hand, the IGT used in this study is a typical affective decision-making task, but it also involves other cognitive functions, such as working memory, executive control, shifting, and declarative memory. The mediating role of the GMV in OFC in the relationship between IGT performance and the GF found in this study was not necessarily the neuroanatomical basis for the hyperfunction in the affective system. On the other hand, the cognitive and affective systems are interactive, interdependent, or even partially overlapping, but we treated them as separate entities in the current study. More attention should be paid to the understanding of the integration and interaction of the two systems underlying the GF in the future. Second, it should be noted that the associations we found were correlational, so it was not clear whether individual differences in behavioral performance were the consequences of the variation in GMVs or the other way around. Finally, this study only explored the neuroanatomical basis of the GF and identified the mediating role of GMV in the cognitive/affective areas. It must be acknowledged, however, that we are unable to infer functional changes in the brain from neuroanatomical alterations.

In conclusion, our findings supported the theoretical model of decision making that highlights the cognitive system's constructive role and the affective system's destructive role in the GF. In other words, the GF seems to result from the cognitive system's hyperfunction (conducive to the implementation of the false belief world model), and the affective system's hypofunction (preventing the creation of somatic markers for the unfavorable options). Our study may enrich the understanding of the neuroanatomical bases of individual differences in the cognitive and affective systems relevant to maladaptive decision making.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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