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Common and distinct neural substrates of the money illusion in win and loss domains

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ABSTRACT

People often evaluate money based on its face value and overlook its real purchasing power, a phenomenon known as the money illusion. In the present study, using functional magnetic resonance imaging (fMRI) combined with a gambling task, we examined the neural signatures of the money illusion in both win and loss domains. Behavioral results showed that self-reported satisfaction with outcomes was modulated by the face value but not the true value of money in both win and loss domains. At the neural level, activity in the posterior insula was associated with the true value of money in the win domain, but not in the loss domain. Importantly, we found that the ventral striatum, ventromedial prefrontal cortex (vmPFC) and amygdala encoded the money illusion in both domains, indicating a domain-general rather than domain-specific neural signature. Moreover, participants with a larger degree of money illusion at the behavioral level showed stronger functional connectivity between the ventral striatum and ventral anterior cingulate cortex (vACC) in the win domain, but stronger functional connectivity between the ventral striatum and amygdala in the loss domain. Our findings highlight the overlapping and distinct neural substrates underlying the money illusion in the context of wins and losses.

1. Introduction

Money is any token that is generally accepted as payment for goods and services. It contains two elements: the face value (i.e., the denomination of the money) and the real value (i.e., the number of items that can be purchased with the money). Economists have documented that individuals' decisions are frequently affected by the nominal rather than the real value of money, a phenomenon known as the money illusion (Cebula, 1981; Mayer and Rozier, 2000; Reinhardt, 1986; Tyran, 2007; Weber et al., 2009). For example, people generally treat 100 dollars today as they did 10 years ago, although the buying power has changed considerably. People are also usually affected by a wage increase but ignore the effect of inflation. The money illusion, a form of irrational thinking (Fehr and Tyran, 2001; Leontief, 1936; Patinkin, 1965), has been shown to affect human behaviors in a variety of experimental and real-world situations (Fehr and Tyran, 2001; Shafir et al., 1997).

In regard to the psychological causes underlying the money illusion, studies indicate that different representations of the same information can lead to different responses (Shafir et al., 1997; Yellen and Akerlof, 2006). For example, people tend to be risk aversive when the outcome is presented as a gain but become risk-seeking when the same outcome is presented as a loss. This cognitive bias is known as the framing effect (Tversky and Kahneman, 1981). Similar to the framing effect, one explanation for the money illusion is that compared to information about money's real value, the nominal representation of money is simpler, more salient and easier to process in the human brain (Shafir et al., 1997).

Although the money illusion is a common phenomenon, its underlying neural mechanisms have not been fully explored. Recently, several studies have shed light on these mechanisms. Our previous study using the event-related potential (ERP) found that participants' reports of the pleasantness of outcomes was modulated by both the face and true values of money. The feedback-related negativity (FRN) was only influenced by the real value of money, indicating that even when participants demonstrate the money illusion at the behavioral level, the human brain may encode the real value of money rapidly at the early stage of decision-making (Yu and Huang, 2013). Another study using functional magnetic resonance imaging (fMRI) found that a change in face value that had no impact on participants' real buying power activated the ventromedial prefrontal cortex (vmPFC), a brain region that is involved in reward anticipation and processing (Weber et al., 2009). However, because the study only compared conditions in which money was identical in real value but differed in nominal terms, it could not provide information

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about the neural encoding of the true value.

It is unclear whether distinct neural substrates are devoted to encoding face versus true values of money. Importantly, it is unclear whether the money illusion recruits a domain-general value encoding network or whether it is associated with domain-specific neural substrates. Investigations on the neural circuits involved in the processing of rewards and punishment have produced inconsistent results. On the one hand, a large number of studies have suggested that monetary gains and losses activate a similar fronto-subcortical network, and differ only in degree (Dreher, 2007; Gottfried et al., 2003; Nieuwenhuis et al., 2005; Tom et al., 2007). On the other hand, some studies have indicated that reward and punishment outcomes may involve different neural substrates (Frank et al., 2004; Yacubian et al., 2006). For example, Yacubian et al. (2006) found that the ventral striatum only represented the computation of expected value and prediction errors in the gain domain, while loss-related expected value and the associated prediction error were represented in the amygdala. Previous studies have emphasized that the findings obtained from the gain domain are not necessarily generalizable to the loss domain (Guo et al., 2013; Wu et al., 2014; Zhou and Wu, 2011). In addition, it is important to distinguish how the brain regions interact in different domains.

In the present study, we used fMRI combined with a simple gambling task to investigate the neural signature and functional connectivity of the money illusion in both win and loss domains. We created different face values and true values of money by manipulating magnitudes and price conditions: For the same magnitude of money in the cheap condition and expensive condition, the face value was identical but real purchasing power differed; for small magnitude in the cheap condition and large magnitude in expensive condition, the true value was identical, but the face value differed (Fig. 1A). We hypothesized that the brain areas that are engaged in computing and experiencing rewards, such as the ventral striatum and vmPFC, would encode the true value and the face value of money. Moreover, besides analytic processes, more intuitive or emotional responses could also play an important role in guiding outcome evaluation. When evaluating monetary winning and losing in complex contexts (i.e., in different price conditions), individuals may rely on heuristics or emotional responses. Thus, we hypothesized that brain regions that are involved in emotional processing, such as the amygdala, might also activate in processing the money illusion.

2. Materials and methods

2.1. Participants

Twenty-five healthy, right-handed participants (11 male; mean age ± SE, 20.36 ± 0.32 years) participated in return for payment. All participants were right-handed and had normal or corrected-to-normal vision. They all reported no history of neurological or psychiatric disorders. The study was approved by the Academic Committee of the School of Psychology at South China Normal University. All participants gave written, informed consent and were informed of their right to discontinue participation at any time. They received a base payment of 60 yuan (about 10 US dollars).

2.2. Experimental paradigm

The experimental paradigm was similar to that in our previous study (Yu and Huang, 2013). Before beginning the task, participants were given the opportunity to familiarize themselves with two shopping catalogs. Each catalog contained 14 items of stationery including a notebook, ruler, pen, etc. All the items in the two catalogs were identical with the exception their price. Prices in the catalog with “cheap prices” ranged from ¥1.4 to ¥2.6 (mean of ¥2), whereas prices in the catalog with “expensive prices” ranged from ¥9.4 to ¥10.6 (mean of ¥10). Participants were then asked to answer several control questions to make sure that they understood the difference between the two catalogs. Participants were told that at the end of the experiment, the money they earned in the following gambling task would not be paid in cash but could be spent on

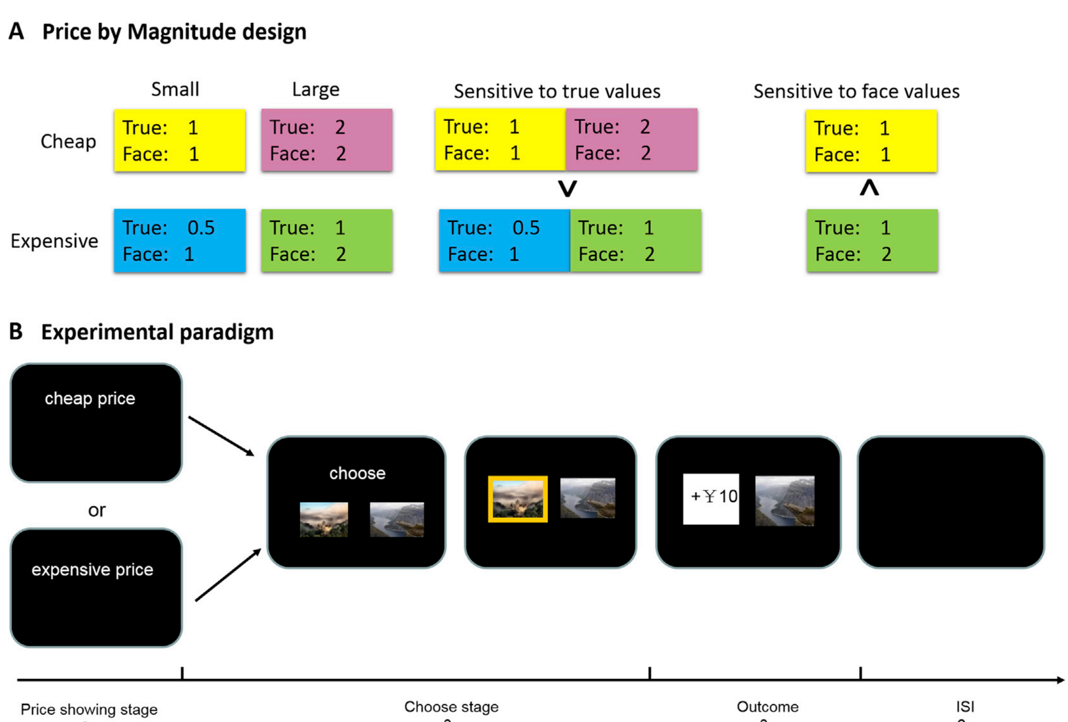

Fig. 1. (A) Study design: price by magnitude of money won (lost). For the same magnitude in the cheap condition and expensive condition, the face value was identical but real purchasing power differed. For small magnitude in the cheap condition and large magnitude in the expensive condition, the true value was identical, but the face value differed. (B) Experimental paradigm. At the beginning of each trial, the cheap price or the expensive price context information was shown. Then participants performed a simple gambling game in which they won (lost) a large or a small magnitude of money based on unpredictable outcomes.

the items in the corresponding catalog.

Participants were asked to complete a gambling task in the MRI scanner. At the beginning of each trial, participants were first presented with the price condition for that trial ("cheap price" or "expensive price"), for 2 s. Then a pair of photos of landscapes without replacement was presented and participants were required to select one of them within 3 s. In the win (loss) block, participants were told that one landscape photo was associated with a large win (loss) and the other landscape photo was associated with a small win (loss), without saying which one. Participants had to guess which photo was associated with the better outcome. The selected photo was highlighted. Then the amount of winning or losing associated with the chosen photo was shown for 3 s. The small magnitude ranged from ¥1.4 to ¥2.6 and the large magnitude ranged from ¥9.4 to ¥10.6. Unbeknownst to the participants, outcomes were predetermined and randomized across conditions. The next trial began 2 s after the offset of the feedback (Fig. 1B). The experiment consisted of 2 win blocks and 2 loss blocks of 28 trials each. Cheap- and expensive-price trials were alternated in small blocks of 7 trials each. The order of win and loss blocks was counterbalanced across participants.

Participants were told that after completion of the experiment, five trials of each condition (expensive and cheap) would be randomly selected for actual payment. Payoffs in the expensive and cheap conditions were separately calculated since these two markets were independent and money in these two different markets is not interchangeable. The accumulated total winnings in each condition could be used by participants to buy things in the corresponding expensive/cheap catalog, i.e., the money earned in the expensive price condition could only be used to buy the items at the price of the expensive catalog and the same way for the cheap price condition. Participants were told that participants that outcomes including losses would also be honored for real money. For example, if one won ¥30 and lose ¥20, he or she would end up with only ¥10. To maximize one's final payoff, participants should gain more money and also try to lose less money. If the total amount of the selected five trials in the expensive or the cheap condition was negative, they could not buy anything.

After the fMRI session, participants were asked to indicate their feelings (satisfaction and surprise) about the eight types of outcomes (e.g., losing/winning ¥10/¥2 in the cheap/expensive price condition) they experienced in the experiment on a 10-point Likert scale ($1 =$ not at all; $10 =$ very intensely). For example, we used questions like "How satisfied (or surprised) did you feel in the following situations?" and underneath the questions we presented eight snapshot images (the outcome stage in Fig. 1B) of the eight types of outcomes.

2.3. Image acquisition and preprocessing

MRI scanning was conducted using a 3.0-T Siemens Allegra scanner. Whole-brain data were acquired with echo planar T2*-weighted imaging (EPI), sensitive to blood oxygenation level-dependent signal contrast (31 oblique axial slices, 3 mm thickness, 3 mm in-plane resolution; repetition time, 2000 ms, echo time [TE], 30 ms). The imaging data were acquired at a 30° angle from the anterior commissure-posterior commissure (AC-PC) line to maximize orbital sensitivity (Deichmann et al., 2003). T1-weighted structural images were acquired at a resolution of $1 \times 1 \times 1$ mm.

Functional image preprocessing was carried out using SPM 12 (www.fil.ion.ucl.ac.uk/spm/). To allow for equilibration effects, the first four volumes were discarded. The EPI images were sync interpolated in time for correction of slice-timing differences and realigned to the first scan by rigid-body transformations to correct for head movements. Utilizing linear and nonlinear transformations and smoothing with a Gaussian kernel of full-width-half-maximum 8 mm, EPI and structural images were co-registered and normalized to the T1 standard template in Montreal Neurological Institute (MNI) space (MNI—International Consortium for Brain Mapping). Global changes were removed by high-pass temporal filtering with a cutoff of 128 s to remove low-frequency drifts in the signal.

2.4. Behavioral data analysis

For the post-experimental satisfaction and surprise ratings, we used repeated measures ANOVA and paired-sample *t*-test to test the true value and money illusion effects at the behavioral level. In line with guidelines offered by Dienes and McLatchie (2018), Bayesian statistics were also used to determine the likelihood and the strength of any effects. We reported both *p* value and Bayes factor, given that frequentist and Bayesian statistics provide complimentary perspectives to addressing the same issues (Lakens, 2017). Bayes factor provide a continuous measure of evidence for one hypothesis (e.g., H1) relative to another hypothesis (e.g., H0). Conventionally, $BF_{10} < 0.33$ have been considered noteworthy evidence for the null hypothesis, while $BF_{10} > 3$ have been considered noteworthy evidence for the alternative hypothesis; values between 0.33 and 3 have been considered as only weak or inconclusive evidence (Jeffreys, 1998). When the Bayes factor is 1, the evidence does not favour either model over the other. To compute Bayes factors, the statistical software JASP was used (JASP, 2018). A default JASP prior for fixed effects was used (r scale prior width $= 0.5$) for Bayesian repeated measures ANOVA and a default Cauchy prior with a scale parameter of 0.5 was used for Bayesian paired-sample *t*-test.

2.5. fMRI data analysis

After preprocessing, statistical analysis was performed using the general linear model. The analysis was performed to establish each participant's voxelwise activation during the outcome presentation epochs. (Onset is at the beginning of each outcome presentation, duration $= 0$.) Activated voxels in each experimental context were identified using an event-related statistical model representing the eight experimental conditions at the outcome stage (winning/losing the small/large magnitude in the cheap/expensive condition), convolved with a canonical hemodynamic response function and mean corrected. Six head-motion parameters defined by the realignment were added to the model as regressors of no interest. Multiple linear regression was then used to generate parameter estimates for each regressor at every voxel. A random-effects analysis (one-sample *t*-test) was performed to analyze data at the group level. Conjunction analysis was performed using the SPM 12 conjunction null function (Friston et al., 2005; Price and Friston, 1997).

In addition to investigating functional localization (which areas are active during a task), we also probe functional interactions between brain areas to understand how information flows between brain areas and how functional areas can change their connectivity under different behavioral circumstances. Psychophysiological interaction PPI analyses was used to measure task-specific increases in the relationship between different brain areas' activity. PPI analyses identify voxels in which activity is more related to activity in a seed region of interest (seed ROI) in a given psychological context, such as during the presence of emotive stimuli. In (PPI) analyses (Friston et al., 1997), each model consisted of a predictor that was time course sampled from one of the regions of interest (ROIs) identified in the experiment (physiological, PPI.Y), a second predictor that was a task-related contrast (psychological, PPI.P) and a third predictor (PPI regressor, PPI.ppi) that consisted of the interaction between the activation and contrast predictors. The fMRI signals within the seed regions were determined using an eigenvector approach after adjusting for variance explained by the six realignment parameters (Büchel and Friston, 1997). Specifically, the first eigenimage, a weighted mean of the ROI, was used in order to address within-ROI functional heterogeneity in which case a single summary measure such as the arithmetic mean may poorly represent activity in the ROI. The first eigenvariate of the extracted BOLD signal was then adjusted by substracting out variance explained by the six realignment parameters (the columns that are all zeros in the 'filtered and whitened' design matrix multiplied with SPM's beta estimates) from the ROI values to remove unwanted variance. The task-related contrast was defined as EWL v.s CWS conditions in the win domain and CLS vs. ELL in the loss domain. The psychophysiological interaction term was calculated as the element-by-element product of the neuronal time series in the source region and a vector coding for the main effect. This means that variance explained by the interaction term is only that over and above what is explained by the main effects of task and physiological correlation. This product was then re-convolved by the canonical HRF. The model also included the main effect convolved by the HRF, the neuronal time series for each source, and the movement regressors as effects of no interest. PPI models were run, and contrast images were generated for positive and negative PPIs. The identified regions had greater or lesser coupling with the source regions according to the context of EWL and CWS conditions in the win domain and CLS and ELL in the loss domain. We sought to identify target regions for which the change in connectivity with the source region varied as a function of behavioral performance (i.e., money illusion). In the higher-order PPI analysis, we included the behavioral money illusion index as a covariate to investigate the relationship between behavioral money illusion effect and functional connectivity in the brain.

To assess the significance of differences in regional activity reported by SPM we performed ROI analyses. In particular, small volume correction (svc) was used on a priori regions of interest, namely reward, negative outcome and emotion processing related regions: the ventral striatum: 6 mm sphere at±14, 10, and −10 (O'Doherty et al., 2004); the ventromedial prefrontal cortex (vmPFC): 6 mm sphere at 12, 47 and 0 (Weber et al., 2009); and the amygdala, the anterior cingulate cortex (ACC), and the anterior and posterior insula, which were defined by the corresponding automated anatomical labeling masks (Tzourio-Mazoyer et al., 2002). Activations in other areas were reported if they survived at $p < 0.001$ uncorrected, cluster size $k > 10$. We also reported regions survived at cluster-level $p < 0.05$ FWE correction based on $p < 0.001$ uncorrected. For display purposes, all images are depicted at $p < 0.005$.

3. Results

3.1. Behavioral results

For the post-experiment self-reported satisfaction with outcomes, a repeated-measures ANOVA using price (cheap vs. expensive), magnitude (small vs. large), and domain (loss vs. win) as independent factors revealed a significant main effect of domain $F(1,24) = 15.24$, $p = 0.001$, $\eta^2 = 0.39$, Bayes factor $(BF_{10}) = 1.53 \times 10^5$. Not surprisingly, participants felt more satisfied with win feedback than loss feedback. The interaction between magnitude and domain was also significant, $F(1,24) = 37.38$, $p < 0.001$, $\eta^2 = 0.61$, $BF_{10} = 3.84 \times 10^{12}$ and the interaction between price and domain was not significant, $F(1,24) = 1.91$, $p = 0.18$, $\eta^2 = 0.08$, $BF_{10} = 0.32$. Specifically, in the win domain, there was no significant difference in satisfaction ratings after winning in the cheap price condition and winning in the expensive condition, $p = 0.12$, $BF_{10} = 0.83$, suggesting that the result is inconclusive. The difference between losing in the cheap price condition and losing in the expensive condition was also not

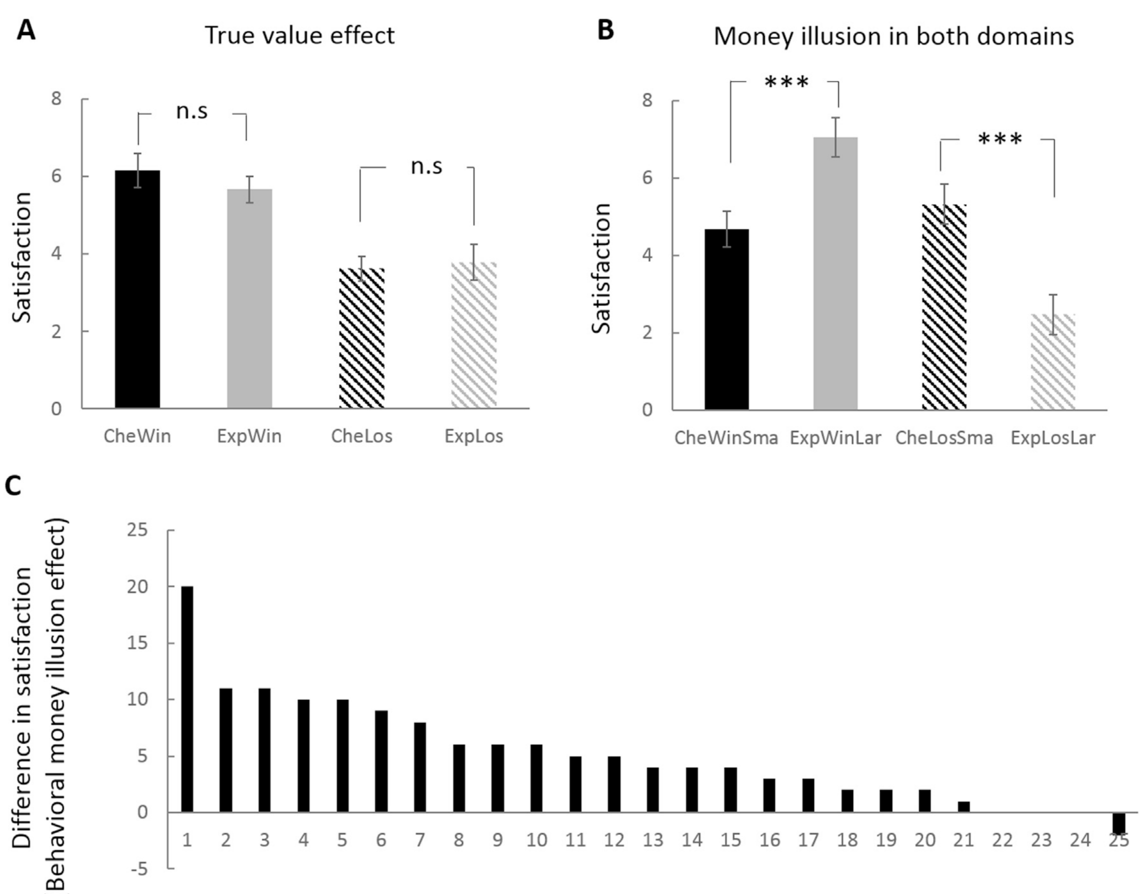

Fig. 2. Post-experiment subjective ratings of satisfaction with outcomes. Outcome evaluation was not influenced by the true value of money (A), while participants exhibited the money illusion in both win and loss domains (B). The money illusion effects seen in each participant are shown in (C) (numerically ordered). The y-axis represents the differences in satisfaction (the difference between win and loss for a large magnitude in expensive condition – the difference between win and loss for a small magnitude in cheap condition). ***$p < 0.001$. Error bars indicate ±1 standard error. CheWin: winning in cheap condition; ExpWin: winning in expensive condition; CheLos: losing in cheap condition; ExpLos: losing in expensive condition; CheWinSma: winning small magnitude in cheap condition; ExpWinLar: winning large magnitude in expensive condition; CheLosSma: losing small magnitude in cheap condition; ExpLosLar: losing large magnitude in expensive condition.

significant, $p = 0.65$, $BF_{10} = 0.31$ (Fig. 2A). These results suggest that the self-reported satisfaction with outcomes was predominately modulated by face value of money, the behavioral effect of true value was very week and inconclusive. All the other effects were not significant, $ps > 0.1$, $0.14 < BF_{10s} < 0.37$.

To test whether there was a money illusion effect on satisfaction in win and loss domains respectively, we compared winning or losing a small magnitude in the cheap price context with winning or losing a large magnitude in the expensive price context (Fig. 2B). Results showed that in the win domain, participants felt more satisfied with winning a large magnitude reward in the expensive condition (mean ± SE, 7.04 ± 0.50) than with winning a small magnitude reward in the cheap condition (mean ± SE, 4.68 ± 0.47), $t(24) = 4.60$, $p < 0.001$, $BF_{10} = 271.00$, although the rewards had the same buying power. In the loss domain, participants also felt less satisfied with losing a large magnitude in the expensive condition (mean ± SE, 2.48 ± 0.52) than with losing a small magnitude in the cheap condition (mean ± SE, 5.32 ± 0.51), $t(24) = 5.00$, $p < 0.001$, $BF_{10} = 527.80$. We also calculated the money illusion effect across both domains for each participant, as (difference in satisfaction scores between winning and losing a large magnitude in the expensive price condition) – (difference in satisfaction scores between winning and losing a small magnitude in the cheap price condition), (EWL-ELL)-(CWS-CLS). For most of the participants (21 out of 25), this calculation resulted in a positive number (5.20 ± 0.96), ranging from −2 to 20, indicating the presence of the money illusion effect (Fig. 2C). Changes in satisfaction in response to price condition also confirm that participants were engaged in the financial gains and losses.

For the self-reported surprise in response to outcomes, a repeated-measures ANOVA revealed a significant main effect of magnitude, $F(1,24) = 25.00$, $p < 0.001$, $\eta^2 = 0.51$, $BF_{10} = 3.06 \times 10^9$, and a significant interaction between price and magnitude, $F(1,24) = 12.28$, $p = 0.002$, $\eta^2 = 0.34$, $BF_{10} = 145.99$. No effects involving domain were significant, $ps > 0.1$, $0.12 < BF_{10s} < 0.30$, suggesting that the satisfaction patterns cannot simply be explained by surprise.

3.2. fMRI results

We analyzed the imaging data of the win and loss domains in separate contrasts to examine the neural signatures of processing the true value of money and of the money illusion (i.e., processing the face value of money). The true value of money was defined by the Cheap_Win (CW) vs. Expensive_Win (EW) and Cheap_Loss (CL) vs. Expensive_Loss (EL) contrasts, where face value was identical but real purchasing power differed. The money illusion was defined by the Expensive_Win_ Large (EWL) vs. Cheap_Win_Small (CWS) and Expensive_Loss_Large (ELL) vs. Cheap_Loss _Small (CLS) contrasts, where the true value was identical, but the face value differed (Fig. 1A). All the significantly activated brain areas are shown in Table 1.

In the win domain, results showed that winning in the cheap condition relative to winning in the expensive condition did not significantly activate any of the brain regions of interest. However, in the reverse contrast, we found that compared with winning in the cheap condition, winning in the expensive condition activated left posterior insula (−45, −12, 12; peak $z = 3.67$, $p_{(FWE)} = 0.035$ svc), suggesting that posterior insula is the brain region encoding the true value of money in the win domain (Fig. 3A). For the money illusion, we found that winning a large magnitude in the expensive condition relative to winning a small magnitude in the cheap condition (EWL vs. CWS) activated bilateral ventral striatum (left: −15, 6, −9; peak $z = 4.72$, $p_{(FWE)} = 0.004$ svc; right: 12, 6, −9, peak $z = 3.23$, $p_{(FWE)} = 0.015$ svc), the vmPFC (9, 48, 3; peak $z = 3.08$, $p_{(FWE)} = 0.023$ svc) and left amygdala (−24, −6, −15; peak $z = 3.20$, $p_{(FWE)} = 0.024$ svc) (Fig. 3B). No significant activation in the brain regions of interest was found for the reverse contrast.

In the loss domain, no brain areas of interest were significantly activated in the contrast associated with the processing of the true value of money, nor for the reverse contrast. For the money illusion, no significant activation was found in the contrast of ELL vs. CLS. However, the reverse contrast (CLS vs. ELL) significantly activated bilateral ventral striatum (left: −18, 9, −6; peak $z = 3.13$, $p_{(FWE)} = 0.02$ svc; right: 12, 6, −12, peak $z = 3.42$, $p_{(FWE)} = 0.006$ svc), the vmPFC (9, 48, 0; peak $z = 2.90$,

Table 1
Brain regions activated at the outcome phase. *Indicates p < 0.05 FWE after small volume correction, #Indicates marginal significance (FWE) after small volume correction. The other regions survived at p < 0.001 uncorrected and a 10-voxel extent threshold. No brain region survived at cluster-level FEW p < 0.05 correction based on p < 0.001 uncorrected.

	Contrast	Brain Regions	Z-score	Peak Coordinate MNI (X, Y, Z)	Volume (voxel)
True value (win)	CW vs. EW	Precuneus	3.53	21, −54, 51	18
	EW vs. CW	Posterior Insula*	3.67	−45, −12, 12	12
		Lateral Ventricle	4.43	3, 12, 18	13
		Transverse Temporal Gyrus	3.67	−45, −12, 12	15
Money illusion (win)	EWL vs. CWS	Ventral Striatum*	4.72	−15, 6, −9	12
			3.67	12, 6, −9	4
		vmPFC*	3.08	9, 48, 3	5
		Amygdala*	3.20	−24, −6, −15	5
		Culmen	4.32	9, −54, −24	16
	CWS vs. EWL	Middle Frontal Gyrus	4.30	39, 3, 42	39
		Superior Parietal Lobule	3.31	30, −57, 51	14
True value (loss)	CL vs. EL	No significant activation			
	EL vs. CL	Sub-Gyral	4.14	−18, −18, 51	17
		Postcentral Gyrus	3.88	−57, −33, 45	22
Money illusion (loss)	ELL vs. CLS	No significant activation			
	CLS vs. ELL	Ventral Striatum*	3.13	−18, 9, −6	3
			3.42	12, 6, −12	10
		vmPFC*	2.90	9, 48, 0	3
		Amygdala*	3.04	−18, −3, −18	9
			3.72	27, −3, −15	30
		Inferior Frontal Gyrus	3.76	60, 18, 12	14
		Medial Frontal Gyrus	3.54	0, 51, 9	32
Money illusion in both domains	EWL vs. CWS ∩ CLS vs. ELL	Ventral Striatum*	3.30	12, 9, −9	24
			3.41	−18, 6, −9	25
		vmPFC**	2.60	9, 48, 3	10
		Amygdala#	2.86	−21, 3, −15	3

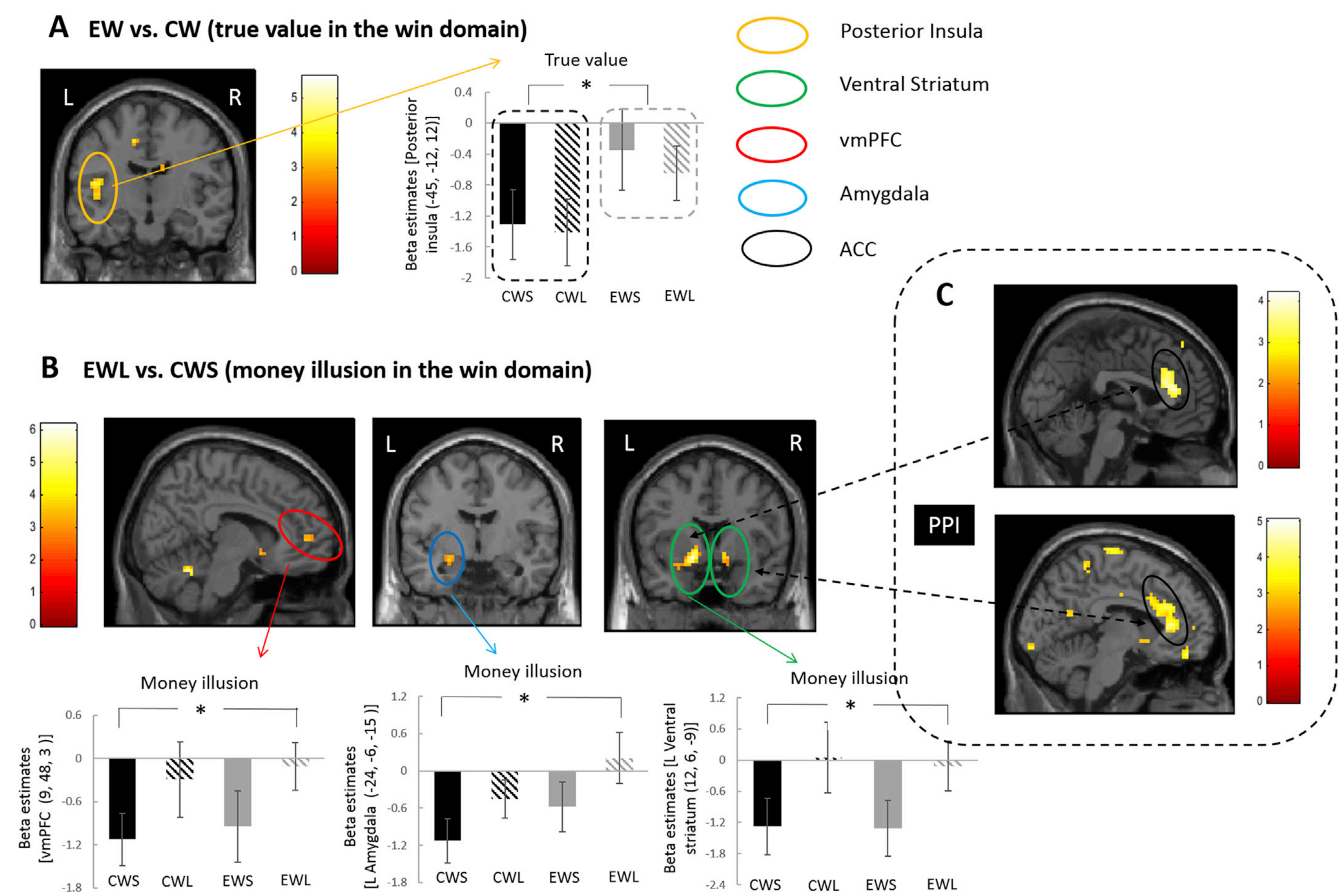

Fig. 3. fMRI results in the win domains. (A) The posterior insula (x, y, z: −45, −12, 12) was significantly activated in the contrast of winning in the expensive condition vs. winning in the cheap condition. (B) Bilateral ventral striatum (left: −15, 6, −9; right: 12, 6, −9), vmPFC (9, 48, 3) and left amygdala (−24, −6, −15) were significantly activated in the contrast of winning a large magnitude in the expensive condition vs. winning a small magnitude in the cheap condition. (C) Participants with a larger degree of money illusion at the behavioral level showed stronger functional connectivity between the ventral striatum and vACC in the win domain. $^{*}p_{(FWE)} < 0.05$. CWS: winning a small magnitude in the cheap condition; CWL: winning a large magnitude in the cheap condition; EWS: winning a small magnitude in the expensive condition; EWL: winning a large magnitude in the expensive condition.

$p_{(FWE)} = 0.035$ svc) and bilateral amygdala (left: −18, −3, −18; peak $z = 3.04$, $p_{(FWE)} = 0.037$ svc; right: 27, −3, −15; peak $z = 3.72$, $p_{(FWE)} = 0.006$ svc) (Fig. 4A).

In order to determine the conjunct neural substrates of the money illusion across both win and loss domains, we performed a conjunction analysis between the EWL vs. CWS and CLS vs. ELL contrasts. Results revealed a significant activation in bilateral ventral striatum (left: 12, 9, −9; peak $z = 3.30$, $p_{(FWE)} = 0.012$ svc; right: −18, 6, −9; peak $z = 3.41$, $p_{(FWE)} = 0.008$ svc). The activations in the vmPFC (9, 48, 3; peak $z = 2.60$, $p_{(FWE)} = 0.066$ svc) and left amygdala (−21, 3, −15; peak $z = 2.86$, $p_{(FWE)} = 0.055$ svc) were marginally significant. These results suggested that bilateral ventral striatum, vmPFC and left amygdala were the conjunct brain regions encoding the money illusion in both win and loss domains.

We further used PPI to examine the task-dependent functional connectivity of the money illusion in each domain. The ventral striatum has a common and prominent role in reward processing and we found that it was activated in the processing of the money illusion in both domains. In addition, the ventral striatum receives synaptic inputs from the orbitofrontal cortex, dorsolateral prefrontal cortex, hippocampus and amygdala (Groenewegen et al., 1999). Thus, we used the ventral striatum as the key region in investigating the functional connectivity of the money illusion. Firstly, we created seed regions using a 6-mm diameter sphere at the left (win domain: −15, 6, −19; loss domain: −18, 9, −6) and right (win domain: 12, 6, −9; loss domain: 12, 6, −12) ventral striatum, regions that were identified in the above contrast analyses. Then we conducted PPI analyses using the money illusion contrasts in each domain (EWL vs. CWS/CLS vs. ELL) with the ventral striatum as a seed. The money illusion at the behavioral level in each domain, based on the post-experimental satisfaction ratings and defined as (EWL – CWS)/(CLS - ELL), was also included as a covariate (results are shown in Table 2).

We found that in the win domain, participants with more money illusion at the behavioral level had stronger functional connectivity between the left ventral striatum and vACC (−3, 30, 18; peak $z = 3.37$, $p(FWE) = 0.014$ svc) and between the right ventral striatum and vACC (−9, 33, 6, peak $z = 4.00$, $p(FWE) = 0.023$ svc, Fig. 3C). In other words, subjects who manifested low levels of money-illusion also had lower levels of coupling between the ventral striatum and vACC in the EWL condition compared to the CWS condition. This demonstrates that it is the change in connectivity induced by winning large in the expensive price condition in comparison with winning small in the cheap price condition (EWL vs. CWS) that is associated with the behavioral money illusion tendency in the win domain. In the loss domain, participants with more money illusion at the behavioral level had stronger functional connectivity between the left ventral striatum and left amygdala (−18, −6, −15, peak $z = 3.40$, $p(FWE) = 0.013$ svc) and between the right ventral striatum and right amygdala (27, 3, −27, peak $z = 3.75$, $p(FWE) = 0.005$ svc, Fig. 4B). The change in connectivity induced by losing small in the cheap-price condition in comparison with losing large in the expensive price condition (CLS vs. ELL) is associated with the

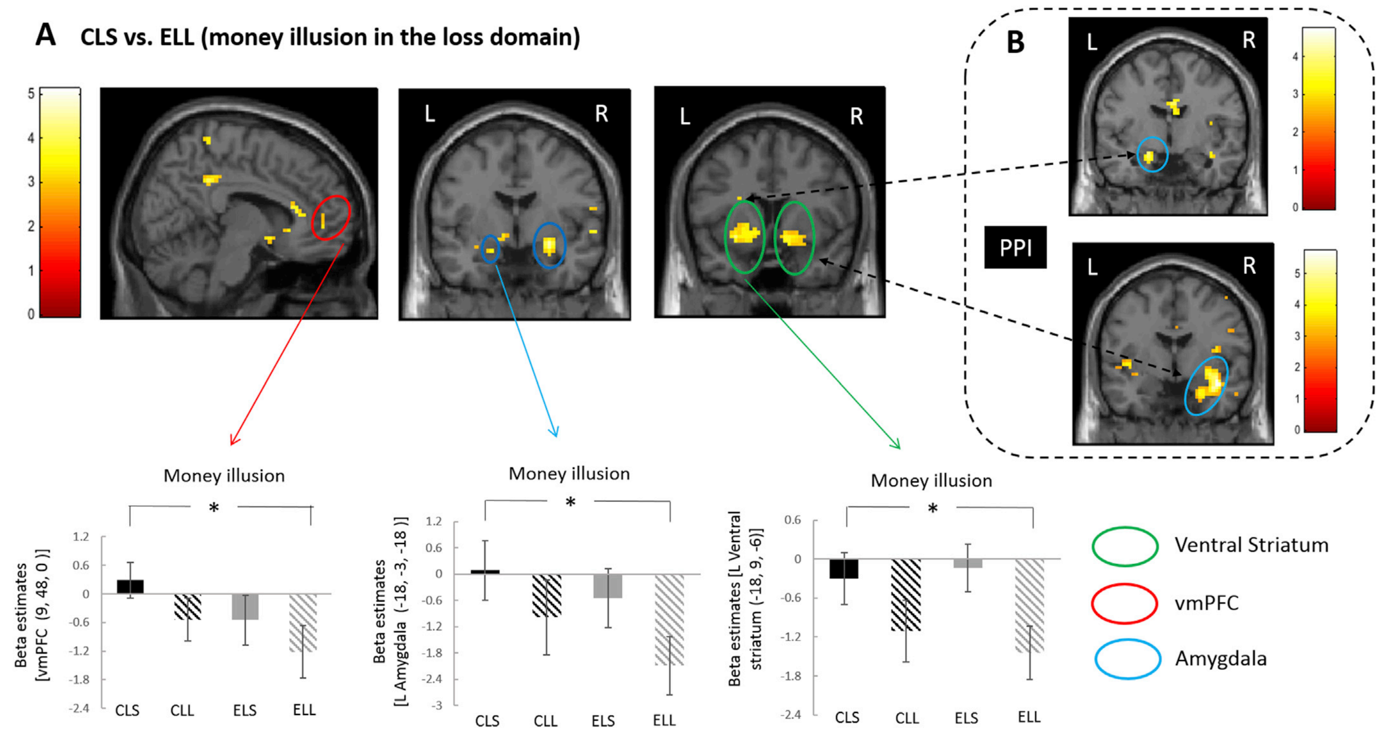

Fig. 4. (A) fMRI results in the loss domain. Bilateral ventral striatum (left: −18, 9, −6; right: 12, 6, −12), vmPFC (9, 48, 0) and bilateral amygdala (left: −18, −3, −18; right: 27, −3, −15) were significantly activated in the contrast of losing a small magnitude in the cheap condition vs. losing a large magnitude in the expensive condition. (B) Participants with a larger degree of money illusion at the behavioral level showed stronger functional connectivity between the ventral striatum and amygdala in the loss domain. *$p_{(FWE)} < 0.05$. CLS: losing a small magnitude in the cheap condition; CLL: losing a large magnitude in the cheap condition; ELS: losing a small magnitude in the expensive condition; ELL: losing a large magnitude in the expensive condition.

behavioral tendencies for money-illusion. Participants who show less money illusion at the behavioral level also show less changes in connectivity between CLS and ELL conditions. Changes in connectivity were identified by regression analyses with behavioral changes, emphasizing the importance of this variable in accounting for the wide range of between-subject variance. These results suggest that the functional connectivity of the money illusion was distinct between the win and loss domains.

4. Discussion

In the current study we investigated the neural signature of the money illusion in the win and loss domains. At the behavioral level, self-rated satisfaction with the outcomes was predominately moderated by the face value of money and individuals demonstrated the money illusion in both win and loss domains. Although our results are inclusive regarding whether true values also modulate self-reported satisfaction, our previous study using the same post-experimental satisfaction evaluation revealed that the self-reported satisfaction was modulated by both face and true values of money (Yu and Huang, 2013). One possibility is that self-reported satisfaction rating is not sensitive enough to measure small effect of true values. Another possibility is that evaluation of true value is more complicated and cognitively-demanding compared with evaluation of face values, as the evaluation of true value requires integration of face value and price information. Participants may simply ignore the true value of money to avoid high cognitive demand. In our study,

Table 2
Functional connectivity of the money illusion contrasts in both domains as a function of behavioral money illusion. The functional-connectivity analysis was conducted using a PPI between EWL and CWS/CLS and ELL conditions with the bilateral ventral striatum as seeds. Money illusion at the behavioral level was defined by the difference of post-experimental satisfaction ratings between EWL and CWS/CLS and ELL conditions. *Indicates $p < 0.05$ FWE after small volume correction. The other regions survived at $p < 0.001$ uncorrected and a 10-voxel extent threshold. ^indicates cluster-level $p < 0.05$ FWE correction based on $p < 0.001$ uncorrected. VS: ventral striatum; L: left; R: right.

Contrast	Seed	Brain Regions	Z-score	Peak Coordinate MNI (X, Y, Z)	Volume (voxel)
EWL vs. CWS	L VS (−15, 6, −9)	vACC*	3.37	−3, 30, 18	20
	R VS (12, 6, −9)	vACC*	4.00	−9, 33, 6	17
		Middle Temporal Gyrus	4.09	63, −12, −3	18
		Sub-Gyral	4.04	−24, −66, 12	13
		Superior Frontal Gyrus^	3.87	3, 39, 54	52
		Transverse Temporal Gyrus	3.793.70	39, −27, 9	18
		Medial Frontal Gyrus	3.59	0, −21, 78	46
		Inferior Parietal Lobule	3.51	42, −24, 27	12
		Middle Temporal Gyrus		−57, −69, 9	11
CLS vs. ELL	L VS (−18, 9, −6)	Amygdala*	3.40	−18, −6, −15	20
		Cingulate Gyrus	3.91	9, −18, 27	16
	R VS (12, 6, −12)	Amygdala*	3.75	27, 3, −27	20
		Posterior Cingulate	3.81	−18, −60, 9	19

participants were given the opportunity to familiarize themselves with two shopping catalogs and were asked to answer several control questions to make sure that they fully understood the difference between the cheap and expensive catalogs, suggesting that they were able to calculate the true values. The cheap vs. expensive information was salient throughout the whole study, making the integration of face value and price less demanding. Nevertheless, the role of cognitive demand in money illusion has rarely been investigated and is definitely worth further investigation in future studies.

At the neural level, the posterior insula encoded the true value of money in the win domain, but no significant activation was found for the processing of true value in the loss domain. Importantly, we found that the ventral striatum, vmPFC, and amygdala were the conjunct brain regions in the processing of the money illusion in both domains, suggesting that the illusion may have common representations of wins and losses. However, the functional connectivity analyses using the ventral striatum as a seed region revealed distinct functional connectivity of brain networks involved in the money illusion across different domains.

In the present study we used an orthogonal design to examine the neural substrates of the face value and the true value of money. We found that compared with winning in the cheap condition, winning in the expensive condition with smaller real buying power activated posterior insula, suggesting that the real value of money is still registered even when participants exhibit the money illusion at the behavioral level. Previous studies have shown that insula is involved in both the experience and the anticipation of negative outcomes (Kim et al., 2006; Seymour et al., 2005) and damage to insula impaired the ability to learn the value of loss-predicting cues (Palminteri et al., 2012). The posterior part of the insula is particularly involved in integrating sensory inputs (Craig, 2009) and is activated in relation to somatosensory stimuli with affective or motivational significance (Deen et al., 2011). In our study, the observed higher brain activation in posterior insula while experiencing smaller real buying power might reflect higher emotional and somatosensory arousal in the context of a potentially greater loss. We did not find any significantly activated brain regions that process the true value of money in the loss domain. Previous studies also failed to identify reliable brain regions encoding values in the loss domain (Brooks and Berns, 2013; Kanayet et al., 2014; Liu et al., 2011). This may be partially due to the limitation of the univariate fMRI approach which is restricted to brain areas in which neuronal activity is relatively uniformly associated with wins/losses across voxels and individuals. Further fMRI studies may use more advanced analysis such as multi-voxel pattern analysis (MVPA) to study brain regions in which neurons represent reward-related information heterogeneously across space and individuals (Kahnt, 2018; Vickery et al., 2011). Researchers have also pointed out the difficulty in studying loss in an lab experimental setting, given that inducing a true financial loss is not allowed by most rules of human experiment (Brooks and Berns, 2013). It is unclear how this asymmetry between win and loss would affect our behavioral and neural results.

A previous fMRI study found that the money illusion activated the vmPFC in the win domain (Weber et al., 2009). Importantly, we extended this finding to the loss domain. Moreover, we found that another brain region, ventral striatum, was also a signature of the money illusion in both domains. Neuroimaging studies have characterized a system of brain regions, including the ventral striatum and vmPFC, involved in processing valuation and experienced reward across a wide variety of contexts (Bartra et al., 2013; Haber and Knutson, 2010; Mobbs et al., 2003; Sabatinelli et al., 2007). It has been proposed that a single neuroanatomical system, known as a 'common neural currency', represents value across modalities including monetary rewards, primary rewards (Kim et al., 2011), and social rewards (Izuma et al., 2008). These studies suggest that vmPFC might function as a hub for processing reward related information, regardless of its sensory properties or valence. The functional significance of this reward processing circuit remains to be further explored. In our experiment, compared with winning a small magnitude in the cheap price condition and losing a large magnitude in the expensive price condition, winning a large magnitude in the expensive condition and losing a small magnitude in the cheap condition were associated with greater activation in reward-related regions. This was true even though the money in these two conditions (cheap and expensive) had the same real buying power, suggesting that the money illusion was associated with a similar reward circuit across win and loss domains.

Several alternative explanations are worth discussing. In the EWL vs. CWS contrast, after controlling for the true value of money, the significant activated brain regions may represent numeric magnitude or nominal monetary value. Numeric-processing neuroimaging studies have also consistently identified intraparietal sulcus in humans and its homologue in monkeys for the representation of symbolic and non-symbolic numeric information (Arsalidou and Taylor, 2011). In a previous study in which numeric and monetary value were independently manipulated, it was found that activity in anterior areas, such as medial orbitofrontal cortex (mOFC), ventral anterior cingulate cortex (vACC), striatum and insula were associated with the increase in monetary value but not the increases in numeric magnitude (Kanayet et al., 2014). The response of posterior parietal cortex, such as intraparietal sulcus has also been shown to encode the numeric magnitude but not monetary reward (Kanayet et al., 2014). Importantly, our findings were cross-domain. It is unlikely that these effects were merely driven by simple numerical differences in reward magnitude which were flipped in the loss domain. Another possibility is that neural money illusion effect was associated with prediction error about true value. The mean true value in each of the cheap and expensive conditions were different and the same true value may elicit different prediction error in the cheap and expensive conditions. This interpretation is in line with the literature showing the adaptive coding of value information in the ventral striatum and vmPFC (Diederen et al., 2016; Lopez-Persem et al., 2016). Further research may use computational modelling to further investigate how true value based prediction error and face value based prediction error guide subsequent decision making.

In addition, the amygdala was found to be involved in the money illusion in both domains. The amygdala has been thought of primarily as a center for the emotion of fear in the brain (LeDoux, 2003); however, a meta-analysis revealed that the amygdala reliably responds to both appetitive and aversive emotional valence stimuli (Ball et al., 2009). More importantly, neuroimaging studies have suggested that the amygdala mediates the performance on many reward-based decision-making tasks. For example, using fMRI combined with the monetary wheel of fortune task, researchers found that the selection of high vs. low reward magnitude increased activity in the amygdala (Smith et al., 2009), which is in line with our current findings. In addition, patients with amygdala lesions have been shown to have a reduction in monetary loss aversion (De Martino et al., 2010). Furthermore, food labels have been shown to bias food evaluations in the amygdala, and the strength of this bias predicted behavioral shifts towards healthier food (Grabenhorst et al., 2013).

Amygdala activation also appears to be related to the strength of the framing effect, suggesting a key role for an emotional system in the processing of decision biases (De Martino et al., 2006). In one study, participants who were homozygous for the short variant of the serotonin transporter gene, which is associated with enhanced amygdala reactivity, also demonstrated an increased framing effect on both behavior and neural activity (Roiser et al., 2009). The money illusion could be an instance of a framing effect in the sense that the real buying power has to be evaluated in different contexts, while the nominal formats are more salient frames that involve a higher activity of the neural emotional system. That possibility is consistent with our finding that the money illusion was associated with amygdala activity in both win and loss domains. Our findings extend current knowledge of the role of the amygdala to include processing the nominal value of money, which provides a convenient way for determining value. Our results also demonstrate an important role for an emotional system in mediating the money illusion.

Furthermore, we found distinct brain networks associated with the money illusion across different domains. Specifically, in the win domain, participants with a larger degree of money illusion at the behavioral level had a stronger functional connectivity between the ventral striatum and vACC. This finding indicates that the changes in coupling between the two regions in response to EWL explain the behavioral individual differences. A task-specific increase in functional connectivity between two regions is suggestive of a task-specific increase in the exchange of information. Invasive tract tracing results in primates demonstrate a unidirectional monosynaptic connection from ACC to the ventral striatum (Haber et al., 1995). Given the vACC's unidirectional projections to the ventral striatum (Cohen et al., 2012; Haber and Knutson, 2010), in the win domain, participants who are more susceptible to money illusion may have more modulation from vACC to the ventral straitum. Similar vACC-striatum modulation has been found to explain social relationship modulated reward processing (Mobbs et al., 2009), supporting vACC's putative role in modulating striatum reward-related processing by providing top–down signals. Human fMRI studies have shown that the vACC plays an important role in reward-based decision making (Bush et al., 2002; Taylor et al., 2006; Williams et al., 2004). A primate study also indicated that cells in the vACC encode reward (Niki and Watanabe, 1979). The functional connectivity between the ventral striatum and vACC seen in the money illusion in the win domain might suggest that an individual who is more sensitive to the face value of money may rely more on this connection to calculate salient rewards (i.e., the nominal value of money). By contrast, in the loss domain, participants with a larger degree of money illusion at the behavioral level had a stronger functional connectivity between the ventral striatum and amygdala. In the loss domain, participants who are more susceptible to money illusion may have more neural modulation from amygdala to the ventral striatum. Amygdala has been shown to project to widespread striatal regions and gate striatal responses (Cho et al., 2013; Fudge et al., 2002). Functional connection between the amygdala and striatum contributes importantly to instrumental learning and performance. Animal studies have shown that disconnection of the amygdala from the striatum lead to impaired sensitivity of instrumental performance to outcome devaluation (Shiflett and Balleine, 2010). Both amygdala and the nucleus accumbens are associated with behavioral inhibition by aversive Pavlovian cues (Geurts et al., 2013). In general, the amygdala seems essential for specific response-outcome associations that underlie goal-directed action (Corbit et al., 2013). Lack of signal input from amygdala to the ventral striatum may actually protect individuals from exhibiting money illusion in the loss context. Researchers have proposed that the critical contribution of the amygdala to reward-based decision making is in eliciting the emotion that is appropriate to winning or losing; the emotion can then be used to guide the value evaluation (Bechara et al., 1996). The functional connectivity in the loss domain may indicate that the money illusion is an illusion at both emotional and cognitive levels, and the emotion-cognition interaction plays an important role in processing the face value of money in the loss domain. Future studies may use advanced effective connectivity methods such as dynamic causal modelling (DCM) to further study the direction of information flow (Friston et al., 2003).

In conclusion, our findings document the neural signature of the money illusion. The money illusion in the win and loss domains both activated similar reward circuits but were associated with distinct functionally connected brain networks. Our findings suggest an intriguing model in which the money illusion in the loss domain reflects a heuristic by which individuals incorporate the emotional information evoked by the nominal value of money into the computational monetary reward process.

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Declaration of interest

None.

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