RESEARCH ARTICLE

Behavioral preference in sequential decision-making and its association with anxiety

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Abstract

In daily life, people often make consecutive decisions before the ultimate goal is reached (i.e., sequential decision-making). However, this kind of decision-making has been largely overlooked in the literature. The current study investigated whether behavioral preference would change during sequential decisions, and the neural processes underlying the potential changes. For this purpose, we revised the classic balloon analogue risk task and recorded the electroencephalograph (EEG) signals associated with each step of decision-making. Independent component analysis performed on EEG data revealed that four EEG components elicited by periodic feedback in the current step predicted participants' decisions (gamble vs. no gamble) in the next step. In order of time sequence, these components were: bilateral occipital alpha rhythm, bilateral frontal theta rhythm, middle frontal theta rhythm, and bilateral sensorimotor mu rhythm. According to the information flows between these EEG oscillations, we proposed a brain model that describes the temporal dynamics of sequential decision-making. Finally, we found that the tendency to gamble (as well as the power intensity of bilateral frontal theta rhythms) was sensitive to the individual level of trait anxiety in certain steps, which may help understand the role of emotion in decision-making.

KEYWORDS

sequential decision-making, electroencephalograph (EEG), independent component analysis (ICA), gambling, anxiety

1 | INTRODUCTION

In many decision-making paradigms, people only need to make a one-shot decision in each trial. As an example, in the simple gambling task designed by Gehring and Willoughby (2002), participants made one selection between high- and low-risk options in each trial. Another major family of decision-making is sequential decision-making with feedback (Wallsten, Pleskac, & Lejuez, 2005). The key features of sequential decision-making are that (a) participants need to make multiple decisions towards an ultimate goal (e.g., income maximization) in the same trial, and (b) each decision generates periodic feedback that functions as a reference of the next decision (Grefenstette, Ramsey, & Schultz, 1990). These features mimic important aspects of real-world human behaviors

(Boorman, Rushworth, & Behrens, 2013; Pleskac & Wershba, 2014). For instance, when playing Stud poker, the player must decide whether or not to continue betting in each round after a new card is shown.

The objective of the current study was twofold. The first aim was to characterize the changes of behavioral preference during sequential decision-making and its associated brain mechanisms. The second aim was to investigate the potential influence of individual anxiety level on sequential decision-making.

1.1 | Behavioral preference and sequential decision-making

The concept of preference has long been debated. Canonical theories indicate that subjective preference is supposed to be stable (see Fox &

Tannenbaum, 2011 for a review). For instance, if a person prefers yellow to blue, then this preference should be relatively insensitive to situational factors. Daily observations and experimental studies, however, suggest that individual preference is subject to situational factors. Take the classic framing effect for example: behavioral preference to an option can be strongly affected by how this option is framed (e.g., worded). Laboratory studies have shown that participants were more likely to choose an option when it was described in terms of potential gains rather than potential losses. In addition, the amygdala (a key region for emotional processing) showed stronger activations in these participants when decisions were consistent with the direction of the framing effect, suggesting that the framing of options affects behavioral preference by modulating emotional states (De Martino, Kumaran, Seymour, & Dolan, 2006; Roiser et al., 2009).

Would subjective preference be affected by periodic feedback during sequential decision-making? (And if yes, then how?) Some behavioral models (e.g., the *target* model) assume that in sequential decision-making tasks, people set a predetermined plan about what to do (e.g., how many rounds to play) before each trial, which would only be updated after the current trial finishes (see Wallsten et al., 2005 for a detailed introduction). In contrast, we argue that human behavior may respond to periodic feedback in a timely manner; for example, a player of Stud poker might be excited by the accumulating rewards and gamble for one more round, or instead quit earlier than planned to preserve these rewards. Supporting the latter possibility, participants became more risk-averse after they have received substantial gains over previous decision steps (Buchel, Brassen, Yacubian, Kalisch, & Sommer, 2011). Indeed, the *learning and evaluation* model, which takes the evaluation of periodic feedback into account, fits the real data much better than the *target* model (Pleskac & Wershbaile, 2014; Wallsten et al., 2005). The success of this model suggests that people are affected by periodic feedback and adjust their behavioral patterns accordingly, which might have evolutionary value for environmental adaptation (Cavanagh, Frank, Klein, & Allen, 2010).

To our knowledge, the psychological and neural mechanisms of the influence of periodic feedback are still largely unclear. To examine the influence of periodic feedback from the perspective of cognitive neuroscience, we investigated if there was any neural index induced by periodic feedback that could be used as a potential predictor for upcoming decisions. Additionally, we sought to interpret the cognitive functions of these neural indexes according to the previous literature.

1.2 | Balloon analogue risk task (BART)

Sequential decision-making paradigms include the BART, the Devil Task, and the Angling Risk Tasks, all of which have similar structures (Pleskac, Wallsten, Wang, & Lejuez, 2008). The current study focused on the BART, because this task has been applied most frequently for its high diagnosticity of maladaptive gambling behavior in clinical research (Lauriola, Panno, Levin, & Lejuez, 2014; Mishra, Lalumière, & Williams, 2010). On each trial of the BART, participants must sequentially decide between pumping up a balloon (gamble) and cashing out (no gamble) in consecutive steps. Choosing the gamble option may

result in successfully inflating the balloon (more bonus accumulated) with another chance of decision, or an explosion (all bonus cleared) (Pleskac, 2008; Pleskac & Wershbaile, 2014). Different steps in the same trial are non-independent, because each step is based on the success (i.e., balloon inflation) of the previous step.

Many cognitive processes have been proposed to be related to the BART, such as attention allocation, response selection, reward processing, and feedback evaluation (Bishara et al., 2009; Pleskac, 2008; Pleskac & Wershbaile, 2014). These hypotheses have been supported by observations of brain activity. Particularly, the following regions are often activated during the BART: the orbital frontal cortex (OFC), which is involved in value encoding and reward processing; the anterior cingulate cortex (ACC), which is involved in response selection and executive control; and the dorsal lateral prefrontal cortex (DLPFC), which is involved in information integration and judgment (Baker & Holroyd, 2011; Helfinstein et al., 2014; Lin, Li, Cazzell, & Liu, 2014; Rao et al., 2014; Telzer, Fuligni, Lieberman, & Galvan, 2013; Weber, Messing, Rao, Detre, & Thompson-Schill, 2014). Meanwhile, event-related potential (ERP) studies have discovered that both the feedback-related negativity (FRN) and P3 component, which are the most important ERP indexes of feedback evaluation (San Martín, 2012), are sensitive to the valence of BART periodic feedback (Euser, van Meel, Snelleman, & Franken, 2011; Fein & Chang, 2008).

To the best of our knowledge, most previous studies averaged the brain signals from different BART steps within the same trial. Consequently, the possible influence of periodic feedback on subsequent behavior has been largely ignored in data analysis of previous investigations. A notable exception is the study of Helfinstein et al. (2014), which found that the activations in the ACC, OFC, parietal, and motor areas in one step predicted whether participants would keep on gambling in the next step. Helfinstein et al. (2014) relied on hemodynamic-based brain-imaging techniques, which suffer from limited temporal resolution and have difficulties in dissociating different processes that may overlap in their time domain (Deshpande, LaConte, Peltier, & Hu, 2009). Inspired by Helfinstein et al. (2014), we recently employed the ERP technique to exploit its exquisite temporal resolution (Amodio, Bartholow, & Ito, 2014). The results showed that larger amplitudes of the P1 and P3 components elicited by periodic feedback indicated that participants would be more likely to gamble in the next step (Gu, Zhang, Luo, Wang, & Broster, 2017b).

1.3 | Methodology of data analysis

ERP signals are based on scalp electroencephalography (EEG), which represents a spatially-mixed signature of brain activity due to the volume conduction effect (van den Broek, Reinders, Donderwinkel, & Peters, 1998). To overcome the mixed-signature concern, the current study combined EEG data with independent component analysis (ICA). The ICA separates mixed signals into temporally independent processes with unconstrained spatial distribution (Makeig, Debener, Onton, & Delorme, 2004; Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997). Brain oscillations in EEG reflect rhythmic fluctuations of populations of neurons, which constitutes a fundamental mechanism for organizing

and coordinating information processing across multiple brain areas during the execution of various cognitive functions (Colgin, 2013). Combined with ICA, electrode-space EEG data can be decomposed into source-space independent component (IC) activities, based on information flows between ICs (Matsumoto & Kakigi, 2014). Here, "information flow" refers to the phenomenon that the information of neural communication flows from upstream brain regions (sources) to downstream ones (destinations) (Kaminski & Blinowska, 1991).

In our opinion, the temporal onset/offset of the information flows between the ICA-based neural sources would lead to a better understanding of the relationship between brain regions during sequential decision-making. We expected that the information flow of neural activity would emerge as follows. First, the occipital visual cortex encodes the perceptual features of periodic feedback. Thereafter, the frontal areas (including the OFC, ACC, and DLPFC) receive the encoded information, evaluate the value of each option, and compare between different options. Finally, the frontal regions drive the motor cortex to prepare for the execution of behavioral actions (see Ernst & Paulus, 2005; Frank, Cohen, & Sanfey, 2009; Platt, 2002 for similar brain models).

1.4 | The potential role of anxiety

The influence of human emotion on behavioral preference is prominent and can be tracked by brain activity (Phelps, Lempert, & Sokol-Hessner, 2014). Among numerous types of emotions, this study focuses on trait anxiety (i.e., the level of anxiety disposition) because of its notable role in decision-making (for reviews, see Hartley & Phelps, 2012; Paulus & Yu, 2012). Individuals with a higher level of trait anxiety are more likely to experience physiological arousal and anxiety-relevant feelings, which in turn affect their behavioral performance (Comte et al., 2015). Many studies have reported that in both real and hypothetical situations, high trait-anxious participants preferred not to gamble, which may be accounted for by heightened anticipatory emotional responses towards uncertainty (Charpentier, Aylward, Roiser, & Robinson, 2017; Eisenberg, Baron, & Seligman, 1995; Giorgetta et al., 2012; Maner et al., 2007). However, a series of our recent studies have revealed that when the "no gamble" option was framed as a potential loss, high trait-anxious participants showed no preference to this option, indicating that their behavioral preference could be interfered with by external information (Gu et al., 2017a; Xu et al., 2013). Regarding the heterogeneous findings in the literature, a plausible explanation is that the relationship between trait anxiety and behavioral preference is dynamic and highly context-dependent. To our knowledge, no prior studies has directly examined anxious people's decision pattern in sequential decision-making, although Lighthall, Mather, and Gorlick (2009) found that acute stress gradually increased the tendency to gamble among male participants in the BART.

1.5 | Experimental hypotheses

In light of the aforementioned findings and the decision-making literature (e.g., Cokely & Kelley, 2009; Weber & Johnson, 2009), we predicted that during the sequential decision-making task (BART), the power of alpha-band (indicating attentional processing), theta-band

(indicating information integration and executive control), and mu (indicating action preparation) rhythms would be sensitive to behavioral preference (measured by "pump ratio;" see below) (Zhang et al., 2014). We also examined the potential effect of trait anxiety on sequential decision-making. However, no directional hypothesis was formulated due to the absence of prior studies on this specific topic.

2 | METHOD

2.1 | Participants

Twenty-four healthy college students (11 males; age = 19.2 ± 1.93 years) were recruited from Shenzhen University as paid participants. All participants were right-handed and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment. The experimental protocol was approved by the local ethics committee (Shenzhen University) and this study was performed strictly in accordance with the approved guidelines.

2.2 | Procedure

Before the experiment, participants were instructed about the rules and the meaning of the symbols in the task. In brief, there were at most three steps for each balloon and participants should choose between "pump" and "cash out" in each step (Figure 1). The probability of balloon inflation versus explosion was 50% versus 50%. Participants were encouraged to respond in a way that would maximize the total score amount. The higher the scores they earned, the more bonus money they would receive at the end of the experiment.

The sequence of stimulus presentation is shown in Figure 1. Each trial began with a 1.5-s preparation screen, followed by a red balloon ($3.0^\circ \times 3.5^\circ$ of visual angle) presented in the center of the screen. There was a question mark inside the balloon, inquiring participants to either inflate the balloon or stop the current trial and cash out the bonus by pressing the "F" or "J" button on a keyboard with their left or right index finger (the button assignments were counterbalanced across participants).

Choosing the "pump" option would result in the disappearance of the question mark for a random interval of 800 to 1,200 ms. Thereafter, if the pumping succeeded, the size of the balloon would increase for 5%. Meanwhile, the amount of current accumulated rewards would also appear inside the balloon. Participants then waited for 1,500 ms until the question mark was presented again, indicating the next opportunity of pumping the balloon (i.e., the next step). In case participants chose "pump" and won in three steps consecutively, a new trial would immediately begin after the presentation of "+20" inside the balloon. If the pumping failed, an explosive mark would appear instead of the balloon to provide a symbolization of exploded balloon, which indicated that the accumulated bonus was cleared in this trial. Then the current trial was finished and a new balloon would be provided (indicated by the presentation of a string "a new balloon"). On the other hand, choosing the "cash out" option would call for another trial immediately, with the accrued bonus points being added to the total scores.

There were totally 500 trials (i.e., 500 balloons) in the experiment. At the end of the task, participants were paid according to the total

FIGURE 1 Illustration of the experimental procedure. This study used the positive feedback in Step 1 (the 5-point balloon) and Step 2 (the 10-point balloon) to predict the decision (pump or cash out) in the upcoming steps. RT: response time [Color figure can be viewed at wileyonlinelibrary.com]

earned points in the task (approximately 80–120 Chinese RMB yuan). The E-Prime (Version 1.1; PST, Inc., Pittsburgh, PA) was used to present stimuli and collect behavioral responses.

Overall, the structure of the formal task was consistent with the original BART, but we made a few modifications to fit the purpose of this study and the requirements of EEG research (Luck, 2004) while retaining the key features of sequential decision-making. First, the number of possible pumps in each trial was decreased to three to ensure that each step had sufficient epochs for EEG analysis. Second, the only difference between Step 2 and Step 3 was outcome variance, but not expected value (i.e., the sum of each possible value multiplies its probability). Third, the expected payoff of each pump and winning probability were made explicit to the participants. See Supporting Information (Part A) for detailed explanations. The practicability of this task design has been confirmed in one of our recent studies (Gu et al., 2017b).

2.3 | Behavioral and anxiety measures

This study calculated the “pump ratio” to measure the individual difference in behavioral preference, dividing the number of gambling decisions (pump) by the total number of decisions (pump + cash out) for each participant.

The level of anxiety was examined by using the Chinese version of the Trait form of Spielberger’s State-Trait Anxiety Inventory (STAI-T), which has demonstrated good internal consistency, reliability, convergent validity, and discriminate validity (Shek, 1993; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983). The STAI-T score ranges from 20 to 80, with a higher score indicating a higher level of trait anxiety.

2.4 | EEG recording and data preprocessing

The EEG was recorded referentially against left mastoid and offline re-referenced to average activities over the scalp, by a 32-channel amplifier (SynAmps, NeuroScan Inc., Herndon, VA) with a sampling

frequency of 250 Hz (32-channel Quik-Cap with sintered Ag/AgCl electrodes). Besides the two electrodes for electrooculogram, 30-channel EEG data were collected with electrode impedances kept below 5 k Ω (ECI Electro-Gel, Electro-Cap International Inc., Eaton, OH).

The recorded EEG data were then offline filtered (1–80 Hz) and segmented from 1 s before to 2 s after the onset of periodic feedback presentation (i.e., the EEG epoch lasted for 3 s). The relatively high cut-off frequency for high-pass filtering was necessary to remove linear trends in the EEG, so as to ensure a reliable result of the ICA (Delorme, Palmer, Onton, Oostenveld, & Makeig, 2012; Jung, Kim, Kim, & Chung, 2005; Matsumoto & Kakigi, 2014). The extended length of epochs was necessary to exclude edge effects when time-frequency analysis is performed (Matsumoto & Kakigi, 2014).

2.5 | ICA procedure

Channel-level analyses are inappropriate to un-mix cortical sources because the inverse problem is heavily underdetermined even for a moderate number of sources (Makeig et al., 2004). The ICA approach greatly simplifies the process of source isolation from the inverse problem of scalp EEG to the estimation of source locations of independent processes with defined scalp projections (Bigdely-Shamlo, Mullen, Kreutz-Delgado, & Makeig, 2013; Delorme et al., 2012). Decomposition of EEG signals by means of ICA enhances the signal-to-noise ratio of data and provides a more functionally-relevant representation of brain dynamics (Makeig et al., 2004; Milne, Scope, Pascalis, Buckley, & Makeig, 2009).

We used EEGLAB 13.5.4b, a free Matlab toolbox developed by Delorme and Makeig (2004), to separate the EEG data into a sum of temporally-independent, spatially-fixed components arising from the brain or extra-brain sources. The ICA algorithm was then performed on individual EEG data to produce 30 independent components (ICs) in each of 24 datasets. To summarize the results of ICA-derived data across individuals, EEGLAB combines ICs from different participants with clustering techniques. This study selected the following IC

characteristics as clustering features: ERP, equivalent dipole location (calculated by DIPFIT 2.2), scalp map, power spectra, and event-related spectral perturbation (ERSP). The ERSP contains narrow-band event-related desynchronization and synchronization and illustrates mean stimulus-locked EEG power deviations from baseline power in decibels (dB) across a broad frequency range (Makeig, 1993). See Supporting Information (Part B) for more technique considerations and parameter settings in the ICA procedure.

2.6 | Information flow analysis

This study used Source Information Flow Toolbox (SIFT; Delorme et al., 2011) to estimate and visualize the information flow between ICA-derived EEG sources. The time-frequency representation of the information flow (direct directed transfer function) was computed individually for each participant, followed by averaging across all participants. See Supporting Information (Part C) for details.

2.7 | Statistics

Descriptive data were presented as arithmetic mean $\pm$ standard deviation (SD). Greenhouse-Geisser and Bonferroni corrections were used whenever appropriate, unless otherwise stated.

Individual measures of ERSP and direct directed transfer functions (DDTF) were first computed, followed by a subsequent bootstrap procedure (extracting at random from baseline data and applied for 500 times) at every pixel (i.e., time-frequency unit). Only significant pixels in ERSP and DDTF plots (two-tailed significance level of $p < .05$) were further considered in a follow-up group level analysis (Cebolla et al., 2015; Ferrarelli et al., 2008; Jenson, Harkrider, Thornton, Bowers, & Saltuklaroglu, 2015). When quantifying the ERSP or DDTF differences between conditions on group level, permutation tests (500 permutations) were performed at every pixel with a strict significance level of $p < .01$ (Jenson et al., 2015; Matsumoto & Kakigi, 2014; Milne et al., 2009; Tsai, Jung, Chien, Savostyanov, & Makeig, 2014). To avoid false positives from multiple comparisons, effects that were significant at less than 20 neighboring time-frequency cells were not interpreted.

Two-tailed Pearson's r correlation was performed between STAI-T score and behavioral/EEG measures (Holm-Bonferroni correction for multiple comparisons).

3 | RESULTS

3.1 | Behavioral results

On average, the 24 participants in Step 1 cashed out in 14.4 trials and pumped up the balloon in 485.6 trials, resulting in 244.2 successful pumps and 241.4 explosions. In Step 2, they cashed out in 77.9 trials and continuously pumped up in 166.3 trials, resulting in 83.0 successful pumps and 83.3 explosions. In Step 3, they cashed out in 52.0 trials and pumped up in 31.0 trials, resulting in 15.6 successful pumps and 15.4 explosions. The numbers of pump versus cash out in each participant are shown in Table 1.

TABLE 1 Trial number in three steps of BART

Subject number	Step 1			Step 2			Step 3		
	Total	Pump	Cash	Total	Pump	Cash	Total	Pump	Cash
1	500	498	2	259	198	61	98	44	54
2	500	500	0	246	130	116	65	17	48
3	500	499	1	251	147	104	66	15	51
4	500	486	14	250	170	80	77	42	35
5	500	433	67	214	176	38	86	49	37
6	500	491	9	235	155	80	75	18	57
7	500	498	2	251	201	50	103	44	59
8	500	498	2	253	210	43	102	59	43
9	500	499	1	251	133	118	68	17	51
10	500	499	1	247	180	67	94	31	63
11	500	497	3	248	115	133	63	11	52
12	500	497	3	256	200	56	110	36	74
13	500	489	11	228	182	46	98	53	45
14	500	498	2	232	184	48	87	10	77
15	500	499	1	260	180	80	91	13	78
16	500	448	52	230	176	54	86	43	43
17	500	490	10	254	171	83	84	37	47
18	500	499	1	243	150	93	75	27	48
19	500	377	123	207	150	57	79	27	52
20	500	474	26	233	138	95	56	25	31
21	500	499	1	266	113	153	68	10	58
22	500	499	1	247	169	78	89	52	37
23	500	487	13	252	207	45	103	54	49
24	500	500	0	248	156	92	69	11	58

The pump ratio was 97.1%, 68.3%, and 36.2% in Steps 1, 2, and 3, respectively (Figure 2A). One-way analysis of variance (ANOVA) revealed a significant effect of step number ($F_{(2,46)} = 192$, $p < .001$, $\eta_p^2 = .893$). Pairwise comparisons showed that the pump ratio significantly reduced from Step 1 to Step 2, and from Step 2 to Step 3 ($p < .001$).

In the whole sample, the trait anxiety score (STAI-T) was 37.0 ± 8.8 (range: 23–61), indicating a medium level of anxiety according to the norm of STAI-T in Chinese college students (43.3 ± 9.2 ; see Li & Qian, 1995). Correlation analyses were performed between the STAI-T score and pump ratio in Step 1 ($r = -.288$, $p = .173$, corrected $p = .173$), Step 2 ($r = .524$, $p = .009$, corrected $p = .027$), and Step 3 ($r = .357$, $p = .087$, corrected $p = .174$). The pump ratio in Step 2 significantly increased as a function of the level of anxiety (Figure 2B).

3.2 | EEG

EEG data in response to the presentation of periodic feedback were collected and analyzed. Our major question was whether the

FIGURE 2 Behavioral results: (A) the pump ratio in three steps; (B) significant correlation between the score of trait anxiety and pump ratio in Step 2

feedback-induced EEG could predict participant's decision (pump or cash out) in the upcoming step. In particular, this study tried to use the feedback in Step 1 to predict the decision in Step 2, and to use the feedback in Step 2 to predict the decision in Step 3. Only the EEG following positive periodic feedback (i.e., successfully pump) were analyzed, because no further action could be taken after negative feedback (i.e., explosion) (see also Helfinstein et al., 2014).

The IC clusters were visually inspected to determine their physiological significance (Matsumoto & Kakigi, 2014). Among the acquired ten IC clusters, seven ones showed significant ERSP differences between the next decision of pump and cash out; they were thus the focus of the following analyses (Figure 3).

In this section, the ERSP data were compared via a two (decision in the upcoming step: pump vs. cash out) by two (step number of the current feedback: Step 1 vs. Step 2) within-subject design. For the sake of brevity, we only report the effects that reach statistical significance.

3.2.1 | Bilateral occipital alpha cluster

The first EEG components that emerged in temporal dimension were left and right occipital alpha clusters (frequency range: 8–13 Hz). The IC properties of the right occipital alpha cluster are showed in Figure 4 (its left counterpart showed similar properties). The Talairach coordinates for the mean dipoles were (−13, −84, 15) and (17, −84, 16) (Figure 4C), which fell within the cuneus [occipital lobe; Brodmann area (BA) 18, secondary visual cortex] in the left and right hemispheres.

In an ERSP map, event-related desynchronization (ERD) indicates a power spectrum reduction while event-related synchronization (ERS) indicates a power spectrum enhancement. For the bilateral occipital alpha clusters, ERSP images in Figure 4D indicate that the alpha spectral power decreased significantly (ERD) during 150 to 900 ms post-feedback, with a larger decrement in feedback-induced EEG epochs followed by pumping compared to cashing out (see the dark red region in the right subplot of Figure 4D, permutation statistics, $p < .01$).

FIGURE 3 EEG topographies of seven IC clusters. These IC clusters are induced by positive periodic feedback (+5 or +10) [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 The IC cluster of right occipital alpha rhythm (8–13 Hz). (A) Mean scalp topography across 24 ICs; (B) equivalent dipole locations of 24 ICs; (C) mean dipole location projected into a standard brain, BA 18, Talairach = (17, -84, 16); (D) mean ERSP images and their differences between the “pumping” and “cashing out” conditions. ERSPs are shown in the frequency range of 1–80 Hz. Colored ERSP images were produced using bootstrap statistics, with red and blue areas indicating power increase and decrease relative to baseline, respectively; green areas indicate nonsignificance ($p > .05$). Binary images show significant ERSP differences between the two conditions based on a permutation test with a significance threshold of $p < .01$; green areas indicate nonsignificance ($p > .01$) [Color figure can be viewed at wileyonlinelibrary.com]

3.2.2 | Bilateral frontal theta cluster

The second EEG components were left and right frontal theta clusters (frequency range: 4–7 Hz). The IC properties of right frontal theta cluster are shown in Figure 5 (its left counterpart showed similar properties). The Talairach coordinates for the mean dipoles were (−32, 34, 40) and (32, 32, 40) (Figure 5C), which fell within the middle frontal gyrus (frontal lobe; BA 9, DLPFC) in the left and right hemisphere. ERSP images in Figure 5D indicate that the theta spectral power increased significantly (ERS) during 270–550 ms postfeedback, with a larger increment in trials followed by pumping compared to cashing out (see the dark red region in the right subplot of Figure 5D, permutation statistics, $p < .01$).

More importantly, the interaction of the two factors (factor 1: decision in the upcoming step; factor 2: step number of the current feedback) achieved significance in the time window of 300 to 500 ms and the frequency range of 4 to 7 Hz (see the blue box in the bottom-right subplot of Figure 6, permutation statistics, $p < .01$). We defined this time-frequency region as the region of interest (ROI). Figure 6 indicates that compared to the ERS induced by Step 1 feedback, the ERS induced by Step 2 feedback displayed stronger intensity; however, this ERS intensity difference only showed significance in the EEG epochs followed by pumping. The interaction was observed in the right (but not the left) frontal theta cluster.

Regarding the interaction shown in Figure 6, correlation analysis was performed between the trait anxiety score and three absolute values (a, Step 1 feedback followed by pumping in Step 2; b, Step 2 feedback followed by pumping in Step 3; and c, feedback in Step 1 and Step 2 followed by cashing out), as well as two relative values [Step 1 followed by (pump – cash out), and Step 2 followed by (pump – cash out)] of the average ERSP within the ROI over the right hemisphere. None of the absolute ERSP values were significantly correlated with the trait anxiety score ($p > .05$). However, the trait anxiety score was positively correlated with the relative values of ERSP (pump – cash out) in Step 2 ($r = .552$, $p = .005$, corrected $p = .025$; Figure 7B) but not in Step 1 ($p > .05$; Figure 7A).

3.2.3 | Middle frontal theta cluster

The third EEG component was middle frontal theta cluster (frequency range: 4–7 Hz), of which the IC properties are shown in Figure 8. The Talairach coordinates for the mean dipole was (−3, 24, 28) (Figure 8C), which fell within the ACC (limbic lobe; BA 24, ventral ACC). ERSP images in Figure 8D indicate that the theta spectral power increased significantly (ERS) during 330 to 650 ms postfeedback, with a larger increment in EEG epochs followed by cashing out compared to pumping (see the dark red region in the right subplot of Figure 8D, permutation statistics, $p < .01$).

FIGURE 5 The IC cluster of right frontal theta rhythm (4–7 Hz). (A) Mean scalp topography across 24 ICs; (B) equivalent dipole locations of 24 ICs; (C) mean dipole location projected into a standard brain, BA 9, Talairach = (32, 32, 40); (D) mean ERSP images and their differences between the “pumping” and “cashing out” conditions. ERSPs are showed in the frequency range of 1–80 Hz [Color figure can be viewed at wileyonlinelibrary.com]

3.2.4 | Bilateral sensorimotor mu cluster

The last EEG components were left and right sensorimotor mu clusters (frequency range: 8–13 Hz). There are two major differences between alpha and mu rhythms. First, the two rhythms have different brain sources; while the alpha wave occurs over the visual cortex, the mu wave occurs over the motor cortex (Pineda, 2005). Second, although the mu rhythm is basically considered as an oscillation in the alpha range, the existence of a concurrent oscillation in the beta range (12.5–30 Hz) has also been suggested (Pfurtscheller & Lopes da Silva, 1999; Pineda, 2005). The IC properties of right sensorimotor theta cluster are showed in Figure 9 (its left counterpart showed similar properties). The Talairach coordinates for the mean dipoles were (−40, −8, 48) and (41, −7, 47) (Figure 9C), which fell within the precentral gyrus (frontal lobe; BA 6, secondary motor cortex) in the left and right hemisphere. ERSP images in Figure 9D indicate that distinct spectral peaks near 10 Hz and 20 Hz were strongly blocked (ERD) during 500 to 1,000 ms post-feedback, with a larger decrement in EEG epochs followed by pumping compared to cashing out (see the dark red region in the right subplot of Figure 9D, permutation statistics, $p < .01$).

3.2.5 | Information flows between EEG sources

Using the Akaike information criteria, the optimal order of multivariate autoregressive (AR) model was determined to be 25.7 ± 11.8 in the 24 participants. The short-time DDTF was then computed based on the AR model to quantify causal connections among the above-mentioned

four EEG IC clusters throughout the time course of feedback presentation (−0.4 to 1.2 s). This procedure resulted in a four by four connectivity matrix with information sources as columns and information destinations as rows (Figure 10). In order to display the matrix of information flows more clearly, for the three pairs of bilateral IC clusters, only the right lateral clusters were involved in this analysis because they showed larger or similar EEG power changes (measured by ERSP) compared to their left counterparts.

Inspection of Figure 10 reveals that the earliest information flows started from the visual cortex (bilateral occipital alpha cluster) to the ACC (middle frontal theta cluster) during 200 to 500 ms within the theta band, and from the visual cortex to the DLPFC (bilateral frontal theta cluster) during 200 to 800 ms within the alpha band. Then the ACC and DLPFC had bidirectional information flows of theta band activity in the time window of 300 to 900 ms (from the DLPFC to the ACC during 300 to 900 ms; from the ACC to the DLPFC during 450 to 850 ms). Approximately at the same time, both regions had causal inputs of theta band activity to the motor cortex (bilateral sensorimotor mu cluster) within the time window of 400 to 900 ms (from the DLPFC to the motor cortex during 400 to 700 ms; from the ACC to the motor cortex during 400 to 900 ms). The cross-region information flows are summarized in Figure 11.

Finally, the DDTF displayed in the information flow matrix (Figure 10) were compared between different steps. Specifically, the intensity of the information flows was compared between Step 1 and Step 2. Permutation tests were performed at every pixel with a significance

FIGURE 6 The IC cluster of right frontal theta rhythm showed significant ERSP interaction of two experimental factors. ERSPs are showed in the frequency range of 1–80 Hz, with significant differences between conditions ($p < .01$) highlighted via a permutation test. The blue box in the bottom-right subplot defines a time-frequency region of interest for correlation analysis [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 7 Correlation between the score of trait anxiety and individual relative values (difference between pumping and cashing out) within the region of interest of ERSP images in the IC cluster of right frontal theta rhythm. (A) Correlation between trait anxiety and relative ERSP values in Step 1; (B) correlation between trait anxiety and relative ERSP values in Step 2

FIGURE 8 The IC cluster of middle frontal theta rhythm (4–7 Hz). (A) Mean scalp topography across 24 ICs; (B) equivalent dipole locations of 24 ICs; (C) mean dipole location projected into a standard brain, BA 24, Talairach = (-3, 24, 28); (D) mean ERSP images and their differences between the “pumping” and “cashing out” conditions. ERSPs are showed in the frequency range of 1–80 Hz [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 9 The IC cluster of right sensorimotor mu rhythm (8–13 Hz). (A) Mean scalp topography across 24 ICs; (B) equivalent dipole locations of 24 ICs; (C) mean dipole location projected into a standard brain, BA 6, Talairach = (41, -7, 47); (D) mean ERSP images and their differences between the “pumping” and “cashing out” conditions. ERSPs are showed in the frequency range of 1–80 Hz [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 10 Information flows among brain regions specified by the IC clusters. Time-frequency matrix of the short-time direct transfer function captures time-varying connectivity between information sources (top row images) and information destinations (left column images). Each pixel shows the information flow relative to the baseline window (−0.4 to 0 s). Red denotes more information flow than the baseline, while blue denotes less. The four brain regions showed as dipoles in the figure correspond to the four EEG IC clusters (see Figures 4, 5, 8, and 9) [Color figure can be viewed at wileyonlinelibrary.com]

level of $p < .01$, which showed that compared to Step 1, Step 2 was associated with a more intensive information flow from the ACC to the DLPFC (Figure 12).

4 | DISCUSSION

4.1 | The mechanisms of sequential decision-making

The behavioral results revealed that participants did not consistently show the same preference across different steps. Instead, the tendency to choose the gamble option (i.e., pump) significantly declined as the step number increased. The EEG data may help explain why participants gradually lost interest in gambling as the step number increased. Four IC clusters (bilateral occipital alpha, bilateral frontal theta, middle frontal theta, and bilateral sensorimotor mu) predicted behavioral decision (pump vs. cash out) in the next step. These findings suggest that behavioral preference could be updated under the influence of periodic feedback, which might be important for behavioral adaptation to a changing environment (Cavanagh et al., 2010; Kennerley & Wallis, 2009).

The first EEG component involved was the occipital alpha oscillations. The up- and down-regulation of alpha-band rhythm is closely

associated with attentional selection of incoming information (Klimesch, 2012; Romei et al., 2008). We suggest that the alpha activity reflected the attentional modulation of visual perception of periodic feedback. Consistent with this idea, dipole source analysis revealed that the alpha cluster was localized in the secondary visual cortex (BA 18; see also simultaneous EEG-functional magnetic resonance imaging (fMRI) studies, for example, Becker, Reinacher, Freyer, Villringer, & Ritter, 2011; Scheeringa, Mazaheri, Bojak, Norris, & Kleinschmidt, 2011). This brain region has been reported to encode various forms of perceptual features and is sensitive to attentional modulation (Kenemans, Lijffijt, Camfferman, & Verbaten, 2002; Sarter, Givens, & Bruno, 2001). Alpha synchronization reflects an inhibitory process that actively suppresses distracting information, that is, the alpha spectral power is inversely correlated with the level of brain excitability (Jenson et al., 2015; Klimesch, Sauseng, & Hanslmayr, 2007; Laufs et al., 2003). Accordingly, stronger alpha desynchronization followed by pumping rather than by cashing out suggests that enhanced excitability of the visual cortex predicts gambling. In our opinion, this phenomenon indicates that increased attentional resources allocated to current feedback presages a stronger willingness to step further during sequential

FIGURE 11 Dynamic information flows between regions of interest. Time durations displayed in blue indicate the significant temporal window of information flows (measured by short-time direct directed transfer function) between EEG IC clusters. Time durations displayed in purple indicate the significant temporal window of EEG activity in each IC cluster (measured by ERSP). The time unit is millisecond (ms) [Color figure can be viewed at wileyonlinelibrary.com]

decisions. In line with the alpha-band results, one of our recent ERP studies using the same paradigm have found that a larger P1 component (which has also been related to attentional selection) indicated a higher likelihood to choose the gamble option (Gu et al., 2017b).

Following the attentional modulations, the bilateral frontal theta and middle frontal theta oscillations performed their functions in a highly interactive manner. ICA-based source localization indicates that the bilateral frontal theta clusters were generated from the DLPFC (BA 9; see similar findings in other EEG and magnetoencephalograph (MEG) studies, for example, Cheyne, Ferrari, & Cheyne, 2012; Ertl, Hildebrandt, Ourina, Leicht, & Mulert, 2013), while the middle frontal theta cluster was generated from the ACC (BA 24; see similar findings in studies using MEG and intracranial recordings, for example, Keil, Weisz, Paul-Jordanov, & Wienbruch, 2010; Smith et al., 2015; Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005). The frontal theta rhythm has been related to important cognitive processes underlying decision-making, such as reward learning, value judgment, and action monitoring

(Baker & Holroyd, 2009; Cavanagh & Frank, 2014; Cohen et al., 2009b; Cohen, Wilmes, & van de Vijver, 2011; Hutcherson, Plassmann, Gross, & Rangel, 2012; Li, Baker, Warren, & Li, 2016; Marco-Pallares et al., 2008). The synchronization of bilateral frontal theta was stronger prior to a pump decision, while the synchronization of middle frontal theta was stronger prior to a cash-out decision. Furthermore, our data suggests that the right frontal theta power was sensitive to step number, such that the synchronization of right frontal theta rhythm enhanced in the latter steps. Accordingly, we propose that the lateral frontal theta (generated from the DLPFC) integrates perceptual information (encoded by alpha-band rhythm) with outcome information, and makes value-guided judgments based on the integration (McClure, Laibson, Loewenstein, & Cohen, 2004; Rorie & Newsome, 2005; Weber et al., 2014). Meanwhile, in fear of the possibility of larger losses, the middle frontal theta (generated from the ACC) inhibits the impulsivity to constantly pursue more rewards (Baker, Wood, & Holroyd, 2016; Cavanagh & Frank, 2014; Garavan, Ross, Murphy, Roche, & Stein, 2002; van de Vijver, Ridderinkhof, & Cohen, 2011). Consistent with our interpretation, Kamarajan et al. (2012) reported that decreased middle frontal theta power was associated with increased impulsivity and risk-taking behavior (see also Pedroni et al., 2017). Our findings could also be compared to those from invasive recording studies in animals (Cohen et al., 2011). Recently, Pedroni et al. (2017) used the Devil Task and found that the EEG oscillations generated from the prefrontal cortex predicted a weaker tendency to gamble in the next trial.

Presumably, the bilateral and middle frontal theta oscillations separately focus on the rewarding and punishing aspects of a decision (Ballard et al., 2011; Cavanagh & Frank, 2014; Luft, Nolte, & Bhattacharya, 2013; Taylor et al., 2006), reflecting a decision-weighting system that makes a tradeoff between positive and negative predictions for future decisions (Cavanagh et al., 2010; Hastie, 2001). It is worth noting that the two frontal regions directly interacted with each other, which was indicated by the bidirectional information flows within theta frequency (Figure 11; see also Cavanagh et al., 2010; Jiang, Zhang, & Gaal, 2015; Luft et al., 2013). Furthermore, the information flow from middle to bilateral frontal regions turned out to be stronger in Step 2 than Step 1 (Figure 12), suggesting that the inhibition function of the middle frontal region is sensitive to outcome variance (see also Gu et al., 2017b). This finding is understandable, seeing that larger outcome variances indicate

FIGURE 12 Information flows from the middle to bilateral frontal regions. Each pixel shows the short-time direct directed transfer function (DDTF) relative to the baseline window (-0.4 to 0 s). Binary images show significant DDTF differences between Step 1 and Step 2 based on a permutation test with a significance threshold of $p < .01$; green areas indicate nonsignificance ($p > .01$) [Color figure can be viewed at wileyonlinelibrary.com]

that the result of gambling would have stronger influence on participants' total earnings. Since the middle frontal theta rhythm encodes the punishing aspect, a larger outcome variance was perceived by this rhythm as an alarm signal of a larger loss, which resulted in a stronger inhibitory effect on the bilateral frontal theta rhythm (see also van de Vijver et al., 2011). These oscillatory dynamics help explain why participants were much more likely to choose the "no gamble" option in the latter steps.

Finally, the mu clusters showed stronger desynchronization in feedback-induced epochs followed by pumping than by cashing out. The two IC clusters were assumed to be located in bilateral sensorimotor cortex (see similar findings in simultaneous EEG-fMRI and MEG studies, for example, Forss & Silen, 2001; Ritter, Moosmann, & Villringer, 2009; see also Zhang et al., 2014). Similar with the alpha rhythm, the power of mu oscillations is negatively correlated with brain excitability (McFarland, Miner, Vaughan, & Wolpaw, 2000; Pfurtscheller, Brunner, Schlogl, & Lopes da Silva, 2006). Therefore, the mu result indicates that a high level of excitability of the sensorimotor cortex is associated with choosing gambling in the upcoming scenario. Considering that the suppression of the mu rhythm over the sensorimotor cortex have been associated with action planning and movement initiation (Leocani, Toro, Manganotti, Zhuang, & Hallett, 1997; Llanos, Rodriguez, Rodriguez-Sabate, Morales, & Sabate, 2013; Pfurtscheller & Berghold, 1989), we propose that, compared to cashing out, choosing gambling is more mentally demanding and needs more resources for action preparation (see also Vickery & Jiang, 2009; Zhang et al., 2014).

This study did not find any significant effect for independent components in the beta (12.5–30 Hz) or gamma (30–80 Hz) band. One might suggest that these results contradict previous findings, given that the importance of the beta-gamma band in decision-making has been confirmed in many other studies. For instance, increased beta-gamma power has been associated with positive rather than negative feedback (Cohen et al., 2009a; Cohen, Elger, & Ranganath, 2007; HajiHosseini, Rodriguez-Fornells, & Marco-Pallares, 2012; Marco-Pallares et al., 2008). Cohen et al. (2007) observed enhanced beta-gamma power following positive feedback in the condition with a lower reward probability (see also HajiHosseini et al., 2012). Marco-Pallares et al. (2008) reported that the beta oscillation was sensitive to the magnitude of positive feedback. Finally, informative feedback induced stronger beta-gamma activity compared to uninformative feedback, indicating the role of this band in reinforcement learning (Li et al., 2016). However, our data analysis did not focus on feedback valence, reward probability, or learning. In our opinion, the null result in the beta-gamma band indicates that this frequency range does not contribute to behavioral preference in sequential decision-making. Regarding the limited sample size of this study, we encourage future research to further explore this issue.

Taken together, the current study highlights the importance of the occipital alpha, bilateral/middle frontal theta, and sensorimotor mu rhythms. Furthermore, the causal connection reveals the temporal relationship between these oscillations. Specifically, more attentional resources allocated to periodic feedback lead to higher activations of the occipital alpha cluster. Perceptual information is then propagated

to the decision-weighting system via long-range theta-band and alpha-band coherence (see also Samthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998) between occipital and bilateral/middle frontal regions. Specifically, the lateral frontal region integrates the sensory input with the information of potential rewards and losses; the middle frontal region, which is in charge of executive control, inhibits an impulse to gamble. Finally, both bilateral and middle frontal regions directly communicate with the sensorimotor cortex via theta-band coherence to shape motor plans and adjust decision on the next encounter (see also van de Vijver et al., 2011).

From a theoretical perspective, one might wonder why behavioral decisions were affected by periodic feedback, as the expected value of each step (reflected by feedback information) remained constant. First, it is worth noting that behavioral preference could be modulated independent of expected value, as the famous St. Petersburg paradox reveals (Weber & Johnson, 2008). Second, periodic feedback in one BART step also functions as the "no gamble" option in the next step. Therefore, it is understandable that participants evaluated this feedback/option to make the next decision (Gu et al., 2017b). Numerous studies using non-sequential tasks have proved that brain activations associated with options could predict participants' decisions (e.g., Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009; Huang, Soon, Mullette-Gillman, & Hsieh, 2014; Hunt et al., 2012; Knutson & Bossaerts, 2007; Leathers & Olson, 2012; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011; Smith et al., 2009). Cohen and Ranganath (2005) found a significant correlation between brain activity and value function in the occipital area during option evaluation. Kahn, Heinze, Park, and Haynes, (2011) found that the DLPFC encodes the variability of reward predictions, which guides subsequent decisions. Knutson, Rick, Wimmer, Prelec, and Loewenstein, (2007) discovered that the activation of the medial prefrontal cortex (including the ACC) associated with the price information of a commercial product is a neural predictor of not purchasing the product (see also Smith et al., 2009). Finally, neural recordings in the sensorimotor area that controls the arm have detected significant activity before a decision between actions is made (see Pastor-Bernier & Cisek, 2011 for a review). The aforementioned brain regions have also long been associated with the BART (Boorman et al., 2013; Helfinstein et al., 2014; Lin et al., 2014; Rao, Korczykowski, Pluta, Hoang, & Detre, 2008; Telzer et al., 2013; Weber et al., 2014). Taking a step further, the current study describes the time course of sequential decision-making by revealing the information flow between these regions, thanks to the excellent temporal resolution of EEG and the application of the ICA method.

4.2 | The role of trait anxiety

The impact of anxiety manifested on both behavioral and EEG results in this study. Specifically, the probability of choosing the gamble option increased as a function of anxiety score in Step 2, which is consistent with our findings that a higher level of anxiety does not necessarily lead to gambling avoidance (Gu et al., 2017a; Xu et al., 2013), and that anxious people might be more impulsive decision-makers (Xia, Gu, Zhang, & Luo, 2017). In the same step, the right frontal theta power

difference between two types of upcoming decisions (gamble vs. no gamble) was also amplified by anxiety. These results are in line with the literature that links trait anxiety with abnormal frontal theta oscillation (Aftanas, Pavlov, Reva, & Varlamov, 2003; Mizuki et al., 1992). We suggest that because larger wins and losses elicit a higher level of arousal (Loewenstein, Weber, Hsee, & Welch, 2001), the impact of anxiety on decision-making becomes more prominent with larger outcome variances. However, since the maximum breaking point was set to three pumps in our task, we do not know whether the anxiety effect would continuously become stronger as a function of outcome variance.

The current findings may enrich the knowledge of sequential decision-making. Bishara et al. (2009) have proposed a mental model of sequential decision-making, which includes a series of factors such as prior belief and payoff sensitivity; emotion is not recognized as an important parameter in that model. Although the association between emotion and BART performance has long been acknowledged, previous studies mostly focused on impulsivity (for a review, see Lauriola et al., 2014). In contrast, this study highlights the importance of anxiety proneness, indicating that various emotional factors modulate sequential decision-making. From a broader perspective, the current findings may also have relevance to the relationship between emotion and decision-making in general. While numerous studies have tried to identify the relationship between specific emotions and behavioral preference (e.g., Lerner, Li, Valdesolo, & Kassam, 2015), few considered the possibility that this relationship might be nonlinear. The current findings reveal that the relationship between anxiety and gambling only manifests on certain steps (Figure 2). This nonlinear relationship indicates that there is a third factor that mediates the interaction between emotion and behavior. Identifying this factor is beyond the scope of the current study, but we suspect that it might have something to do with the function of emotional regulation. Heilman, Crişan, Houser, Miclea, and Miu (2010) have found that while negative emotions strengthen the preference to “no gamble” in the BART, emotional regulation strategies significantly impede this effect.

5 | LIMITATIONS

The technical limitations of this study should be noted. First, although we used ICA to minimize the contribution of volume conduction to scalp EEG, the relatively low accuracy of EEG source localization may still have affected the reliability of our conclusions (Zhukov, Weinstein, & Johnson, 2000). Follow-up research using alternative techniques (such as simultaneous EEG-fMRI, MEG, and intracranial EEG) would be needed to verify the neural substrates found in this study. Second, the DDTF does not exclude the possibility that information flow from region A to region B has passed through other regions before it ultimately reaches B. Therefore, our neural model should be regarded as a sketch that only captures the most important nodes of the brain systems involved in sequential decision-making. Further investigation is awaited to add-in more details to the current model with more details. Finally, this study focused on prediction analysis between neighboring steps in the same trial (see also Gu et al., 2017b). Regarding the success

of between-trial analysis in previous EEG studies (Cohen et al., 2007; Cohen & Ranganath, 2007; Peterson, Lotz, Halgren, Sejnowski, & Poizner, 2011; Zhang et al., 2013), it would be interesting to compare the efficiency between within-trial and between-trial analyses. Nevertheless, since the pump ratio at the beginning of each trial was close to 100%, the number of “cash out” samples was not enough to train a classifier. Therefore, it is not applicable to use EEG signals associated with the final feedback to predict decision-making in the next trial. We suggest future studies address this issue using an alternative task design.

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SUPPORTING INFORMATION

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