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Blunted neural responses to monetary risk in high sensation seekers

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ABSTRACT

The sensation-seeking trait is a valid predictor of various risk-taking behaviors. However, the neural underpinnings of risk processing in sensation seeking are yet unclear. The present event-related potential (ERP) study examined electrophysiological correlates associated with different stages of risky reward processing in sensation seeking. Twenty-one high sensation seekers (HSS) and 22 low sensation seekers (LSS) performed a simple two-choice gambling task. Behaviorally, whereas LSS exhibited a risk-averse pattern, HSS showed a risk-neutral pattern. During the anticipation stage, an increased stimulus-preceding negativity was elicited by high-risk compared to low-risk choices in LSS but not in HSS. During the outcome-appraisal stage, the feedback-related negativity, when calculated as the difference between losses and gains, was enhanced in response to the high-risk versus low-risk outcomes, which appeared for LSS but not for HSS. Further, HSS as compared to LSS exhibited a diminished P300 to both gains and losses. These findings suggest that risk-taking behavior in sensation seeking is expressed as blunted neural responses to risk in the anticipation stage and in the outcome-appraisal stage, which represents a candidate target for drug prevention.

1. Introduction

The sensation seeking personality trait is a predictor of substance use and other risky behaviors (Zuckerman, 2007), and hence becomes a potential target for drug-prevention programs in recent years (Everett and Palmgreen, 1995; Sargent et al., 2010). High sensation seekers (HSS), compared to low sensation seekers (LSS), are more likely to pursue exciting, but potentially risky, behaviors, including drug use, reckless driving, excessive gambling, promiscuous sexual activity, and even suicidal behavior (Bardo et al., 2007; Roberti, 2004; Zuckerman, 2007). However, the mechanism underlying risk taking in sensation seeking remains largely unexplored.

Traditionally, behavioral differences between HSS and LSS can be attributable to individual differences in an optimal level of arousal (Zuckerman, 1969, 1984). This theory is related to the inverted-U curve between arousal and performance (Hebb, 1955). Different arousal level leads people to seek or avoid stimulation to maintain his/her arousal at an optimal level (Eysenck, 1967). HSS, as compared to LSS, have a sub-optimal level of arousal towards daily routines and thus need more stimulation to reach and maintain their optimal level of arousal. As such, HSS compared to LSS may be more vulnerable to various risk-taking behaviors.

However, recent theories highlight the role of motivation in sensation seeking and hold that sensation-seeking behaviors are driven by a hyperactive approach system (Joseph et al., 2009; Kruschwitz et al., 2012) and a hypoactive avoidance system (Lissek et al., 2005; Zheng et al., 2014). For instance, HSS versus LSS tend to exhibit an enhanced sensitivity to the reinforcing effect of psychostimulant drug (Kelly et al., 2006; Stoops et al., 2007) and a blunted response to error (Santesso and Segalowitz, 2009; Zheng et al., 2014). Recently, functional magnetic resonance imaging (fMRI) studies have found that HSS relative to LSS show enhanced activation following receipt of monetary reward (Kruschwitz et al., 2012), but reduced activity when receiving punishment (Kruschwitz et al., 2012) or the absence of reward (Cservenka et al., 2012).

Converging evidence has demonstrated that reward processing is not a homogenous construct, but can be parsed at least into distinct anticipation and outcome-appraisal stages (Berridge and Robinson, 2003; Knutson et al., 2001; Waugh and Gotlib, 2008). With its fine-grained temporal resolution, event-related potential (ERP) technique is uniquely suitable to investigate in detail the time course of reward processing in sensation seeking since it can permit the separation of neural events occurring very closely in time (Luck, 2014), such as reward anticipation and outcome appraisal (Foti and Hajcak, 2012; Zheng et al., 2015).

Reward anticipation can be indexed by the stimulus-preceding

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negativity (SPN; Brunia et al., 2011), a slow negative-going wave that progressively increases in amplitude prior to the presentation of feedback. This component is thought to primarily originate in the insular cortex (Bocker et al., 1994; Brunia et al., 2000; Kotani et al., 2009) and constitute an index for anticipatory, dopaminergically mediated brain response (Foti and Hajcak, 2012; Mattox et al., 2006; Zheng et al., 2015). In contrast, outcome appraisal can be indexed by the feedback-related negativity (FRN) and P300 (Gehring and Willoughby, 2002; Kamarajan et al., 2009; Yeung and Sanfey, 2004). The FRN is a frontocentral negativity occurring between 250–350 ms following the presentation of feedback and appears to be generated in the anterior cingulate cortex (Gehring and Willoughby, 2002; Miltner et al., 1997) and in the striatum (Carlson et al., 2011; Foti et al., 2011). Traditionally, the FRN is thought to reflect an early, binary evaluation of outcomes as either better or worse than expected (Holroyd and Coles, 2002), or a rapidly evaluation of the motivational significance of outcomes (Gehring and Willoughby, 2002). However, recent evidence has proposed that variation in the FRN amplitude may be driven by reward outcome (Proudfit, 2015). The P300 is a positive deflection occurring between 350–600 ms after feedback presentation with a parietal distribution and has been associated with attentional resources involved in stimulus evaluation based on motivational significance (Donchin and Coles, 1988; Nieuwenhuis et al., 2005).

To our knowledge, however, no ERP study in sensation seeking has investigated the neural correlates of reward processing during different stages, thus limiting understanding of temporal dynamics of incentive processing in sensation seeking. The present study sought to address this issue. To this end, we examined the reward processing in HSS as compared to LSS while they subjectively anticipated and experienced rewards. HSS and LSS made a choice between a low-risk option and a high-risk option during a simple gambling task. Behaviorally, we predicted that HSS would tend to make high-risk decision compared to LSS. Importantly, we predicted that the behaviorally reduced sensitivity to risk in sensation seeking would be represented in the anticipation stage as indexed by the SPN and in the outcome-appraisal stage as indexed by the FRN and P300. According to the arousal theory, HSS compared to LSS would exhibit reduced risk effect for these ERP components. On the other hand, if the motivational theory is correct, we expected that larger ERP components would be observed for positive rewards but smaller ERP components would be obtained for negative rewards in HSS relative to LSS.

2. Materials and methods

2.1. Participants

Forty-three participants were recruited from the student population of the Dalian Medical University. Participants were initially selected from a group of 783 responders on the basis of their scores on the Sensation Seeking Scale Form V (SSS-V; Zuckerman et al., 1978). The SSS-V consists of four subscales (10 items each): thrill and adventure seeking (a desire to participate in physically risky activities), experience seeking (search for new experiences through a nonconformist manner), disinhibition (an interest in socially and sexually disinhibited activities), and boredom susceptibility (an aversion to monotony and repetitiveness). Summing all the 40 items derives an overall sensation-seeking score. This scale has demonstrated good reliability and validity in Chinese culture (Wang et al., 2000).

Responders who scored high in sensation seeking (in the upper 20% of the distribution) were assigned to the high sensation-seeking group, whereas the responders who scored low (in the lower 20% of the distribution) were assigned to the low sensation-seeking group. Potential participant was excluded if he/she was suffering or had suffered from any neurological or psychological disorders or if he/she had any history of drug use. All participants were right-handed and had normal or correct-to-normal visual acuity. Participants also completed the Impulsive Sensation Seeking Scale (Zuckerman et al., 1993), the Barratt Impulsiveness Scale (Version 11, Patton et al., 1995), the Behavioral Inhibition System/Behavioral Approach System Scales (Carver and White, 1994), and the Temporal Experience of Pleasure Scale (Gard et al., 2006). Each received a base payment of 30 yuan for participation, plus a bonus of 30 yuan on the basis of their earnings in the task. Written, informed consent was obtained from each participant, and the study was approved by the local ethics committee.

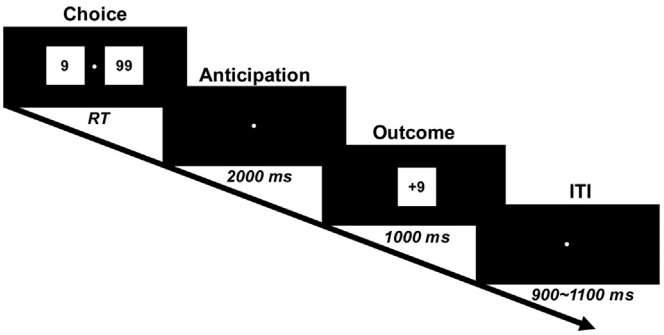

Fig. 1. Schematic representation of a simple two-choice gambling task. ITI = intertrial interval.

2.2. Procedure

The participants were seated comfortably in a dimly lit and sound-attenuating chamber approximately 80 cm away from a computer screen. Each trial (Fig. 1) began with two options (the numeral 9 and 99, indicating the gambling points) that appeared on either side of a fixation point. The participants then selected one of the two alternatives by pressing a button, corresponding to the location of the chosen option, with either their left or right index finger. This pair of options remained on the screen until the participants made a choice. Following their response, a fixation point was presented in the center of the screen for 2000 ms and, thereafter, a number (either positive or negative) appeared for 1000 ms to indicate how many points they won or lost on the trial. Each trial finished with an intertrial interval varying randomly from 900 to 1100 ms. The task consisted of 480 trials divided into six blocks (80 trials each), and a short break was given between blocks. A practice block with 10 trials was used before the formal experiment in order to familiarize the participants with the procedure.

Since risk can be interpretable in terms of the mean squared deviation from the expected outcome (Markowitz, 1952), the option "9" was defined as the low-risk option that yielded either a gain of 9 points or a loss of 9 points, whereas the option "99" is defined as the high-risk option that yielded either a gain of 99 points or a loss of 99 points. Moreover, the probabilities of the outcomes of each option were equivalent, making the expected value of each option zero. Before the formal experiment, the participants were encouraged to use any strategy they wanted to maximize the amount of points. The higher the points they earned, the more bonus money they would receive. However, information regarding the conversion from points to money was not provided until the end of the experiment.

2.3. Recording and analysis

Electroencephalogram (EEG) signals were recorded from 30

sintered Ag/AgCI electrodes (FP1, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T3, C3, Cz, C4, T4, TP7, CP3, CPz, CP4, TP8, T5, P3, Pz, P4, T6, O1, Oz, and O2). Electrodes were mounted on an elastic cap according to the extended 10–20 system. The EEG signals were referenced online to the right mastoid electrode, and then re-referenced offline to the mean of the activity at the left and right mastoids. Horizontal electrooculogram (EOG) was recorded as the voltage from electrodes placed at the external canthi of both eyes to monitor horizontal eye movements. Vertical EOG was recorded via a pair of electrodes placed on the left infraorbital and supraorbital areas to detect blinks and vertical eye movements. All electrode impedances were <5 K Ω. The EEG and EOG were amplified and digitalized using a Neuroscan NuAmps amplifier with a sampling rate of 500 Hz and a low-pass filter at 100 Hz in DC acquisition mode.

The EEG data were preprocessed and analyzed using MATLAB 2011a (MathWorks, US) and EEGLAB toolbox (Delorme and Makeig, 2004). Following previous research (Donkers et al., 2005), the original EEG signals were filtered twice using different parameters with a low-pass at 20 Hz for SPN analysis and a band-pass of 0.1 and 20 Hz for FRN and P300 analysis to minimize the possible interferences from the SPN. Both the filtered EEG data were then segmented into epochs that were time-locked to the feedback onset. For the SPN, epochs began 2000 ms prior to and ended 500 ms post the feedback onset, with the activity from –2000 to –1800 ms serving as the baseline; for the FRN and P300, epochs included 200 ms pre-feedback activity and extended 1000 ms post-feedback, with the activity from –200 to 0 ms serving as the baseline. The epoched data for each participant were screened manually for artifacts (e.g., spikes, drifts, and non-biological signals) and then were subjected to an informax independent component analysis (runica) (Delorme and Makeig, 2004; Jung et al., 2001) and, thereafter, blink components were manually selected and removed. In all datasets, the blink components had a large EOG channel contribution and a frontal scalp distribution. For the resulting data, epochs belonging to the same condition were averaged together for each participant.

According to the grand average waveforms and topographic maps, the SPN was scored as the mean amplitude from –200 to 0 ms (i.e., the 200 ms window immediately before the feedback onset) at lateral electrode sites (FT7/8 and T3/4), where the SPN was maximal. To isolate the FRN component, we created a difference waveform for low-risk outcomes (losses minus gains following low-risk choices) and a difference waveform for high-risk outcomes (losses minus gains following high-risk choices) (Holroyd et al., 2009; Walsh and Anderson, 2011), which could minimize the overlap between the FRN and other ERP components (Luck, 2014). The FRN was extracted as the mean activity of the difference waveforms from 250 to 350 ms after the feedback onset at Fz and FCz where it was maximal. P300 was scored as the mean voltage from 350 to 450 ms post the feedback onset at CPz and Pz due to a posterior distribution.

All the ERP data were analyzed in separate repeated-measures analysis of variance (RMANOVA). The SPN data were analyzed using group (HSS vs. LSS) as between-subject factor and risk (9 vs. 99), hemisphere (left vs. right), and site (FT7/8 vs. T3/4) as within-subject factors. The FRN data were analyzed with a Group $\times$ Risk $\times$ Site (Fz vs. FCz) RMANOVA. A Group $\times$ Valence (gain vs. loss) $\times$ Risk $\times$ Site (CPz vs. Pz) RMANOVA was applied to the P300 data. Statistical analyses were conducted using SPSS (Version 19.0) software. Main effects or interactions involving hemisphere or site are not reported as they are not theoretically relevant to the present study. Greenhouse–Geisser epsilon (G–GE) correction was used for all comparisons with more than two within-subject levels (Jennings and Wood, 1976). Post hoc comparisons were corrected using the Bonferroni procedure and only corrected p values were reported. The partial eta-squared (η_p^2) was also reported as a measure of the proportion between the variance explained by one experimental factor and the total variance.

3. Results

3.1. Demographic and behavioral data

Table 1 shows the demographic data for high and low sensation-seeking groups, respectively. The group did not differ on age, gender, and educational level ($ps > .05$). As expected, the groups differed significantly on overall sensation-seeking score and its subscale scores ($ps < .0001$). Moreover, HSS scored higher on impulsive sensation-seeking score and its subscale scores, motor-impulsivity score, drive score, fun seeking score, and anticipatory pleasure score than LSS ($ps < .05$).

HSS and LSS earned similar points in this task, $t(41) = -0.46$, $p = .649$. Although the average decision-making time for high-risk option was shorter for HSS relative to LSS (Fig. 2A), this result failed to reach significance, $F(1, 41) = 1.10$, $p = .299$, $\eta_p^2 = .03$. As expected, the average proportion of making risky decisions (Fig. 2B), which was computed as the number of times that participants chose the 99 option divided by the total number of choices, was higher for HSS than for LSS, $t(41) = 2.96$, $p = .005$. Specifically, LSS made significantly fewer risky decisions than the chance level (0.5), $t(21) = -3.19$, $p = .004$, indicating a risk-averse pattern. In contrast, HSS exhibited a risk-neutral pattern, $t(20) = 0.95$, $p = .355$. Further conditional analysis was performed to examine how risk preference was influenced by the outcome on the

Table 1
Sample characteristics (M ± SD).

	High sensation seekers ($n=21$)	Low sensation seekers ($n=22$)	p value
Gender (M/F)	10/11	11/11	.876
Age (years)	22.67 ± 0.66	22.23 ± 0.81	.059
Education (years)	15.43 ± 0.81	15.23 ± 0.92	.452
SSS-V			
Thrill and adventure seeking	8.38 ± 1.56	2.68 ± 1.52	< .001
Experience seeking	7.05 ± 1.32	1.59 ± 1.26	< .001
Disinhibition	5.90 ± 0.83	1.32 ± 1.32	< .001
Boredom susceptibility	4.71 ± 1.59	1.00 ± 0.98	< .001
Sensation seeking	26.05 ± 1.83	6.59 ± 1.84	< .001
ImpSS Scale			
Impulsivity	3.24 ± 1.73	1.09 ± 1.19	< .001
Sensation seeking	7.24 ± 1.04	2.59 ± 1.79	< .001
Impulsive sensation seeking	10.48 ± 2.09	3.68 ± 2.50	< .001
BIS-11			
Attention	18.90 ± 1.41	18.64 ± 2.01	.617
Motor	23.62 ± 2.73	20.95 ± 2.77	.003
Non-planning	30.24 ± 3.35	31.18 ± 2.87	.326
Impulsivity	72.76 ± 5.21	70.77 ± 6.06	.256
BIS/BAS scales			
BIS	19.86 ± 2.39	20.86 ± 2.21	.159
Drive	12.38 ± 1.60	11.14 ± 1.42	.010
Fun seeking	15.86 ± 2.03	12.95 ± 1.91	.000
Reward responsiveness	13.29 ± 1.38	13.14 ± 1.81	.763
TPES			
Anticipatory pleasure	40.14 ± 5.95	35.14 ± 6.39	.011
Consummatory pleasure	47.95 ± 6.35	43.64 ± 7.75	.053

Note. SSS-V, Sensation Seeking Scale Form V; ImpSS, Impulsive Sensation Seeking; BIS-11, Barratt Impulsiveness Scale, Version 11; BIS/BAS, Behavioral Inhibition System/Behavioral Approach System; TPES, Temporal Experience of Pleasure Scale.

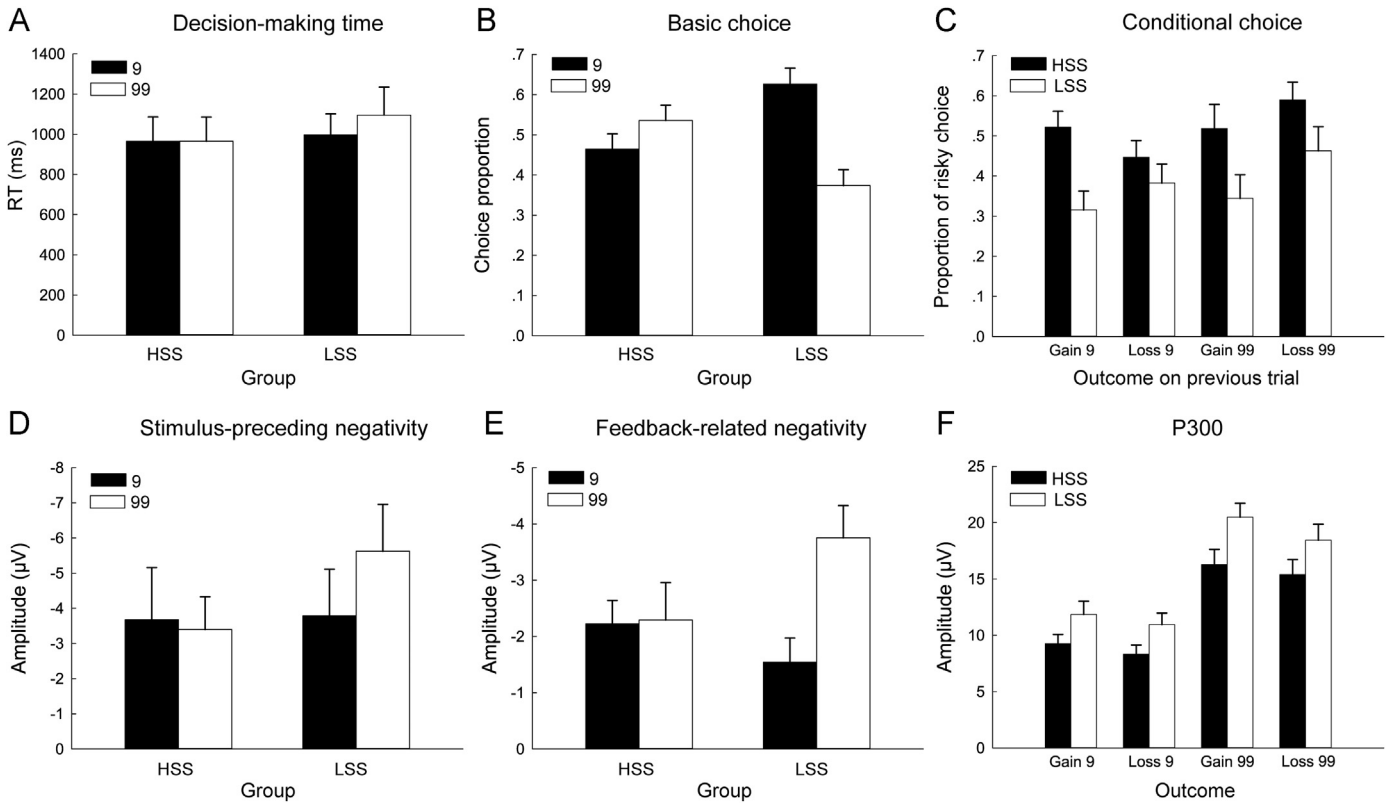

Fig. 2. Behavioral data ((A) decision-making time; (B) choice proportion; (C) the effect of preceding outcome on the riskiness of behavior) and ERP component data ((D) stimulus-preceding negativity; (E) feedback-related negativity; (F) P300) for high sensation seekers (HSS) and low sensation seekers (LSS). Standard errors are also depicted. The ERP data were averaged across the electrodes selected for analysis.

previous trial (Fig. 2C). Although the group effect was significant, $F(1, 41)=7.38$, $p=.010$, $\eta_p^2=.15$, no interaction involving group was significant ($ps > .05$), indicating that both groups were similarly influenced by the outcome on the previous trial. Both HSS and LSS tended to take a high-risk option when the previous choice was a high-risk one than when it was a low-risk one, $F(1, 41)=4.22$, $p=.046$, $\eta_p^2=.09$.

3.2. Electrophysiological data

3.2.1. SPN

Fig. 3 displays grand average ERP waveforms following decision making until the feedback onset and topographic maps of the SPN (−200 to 0 ms). Consistent with previous research (Brunia et al., 2011), both groups showed a typical SPN that developed gradually as a relative negativity after the choice and reached its maximum

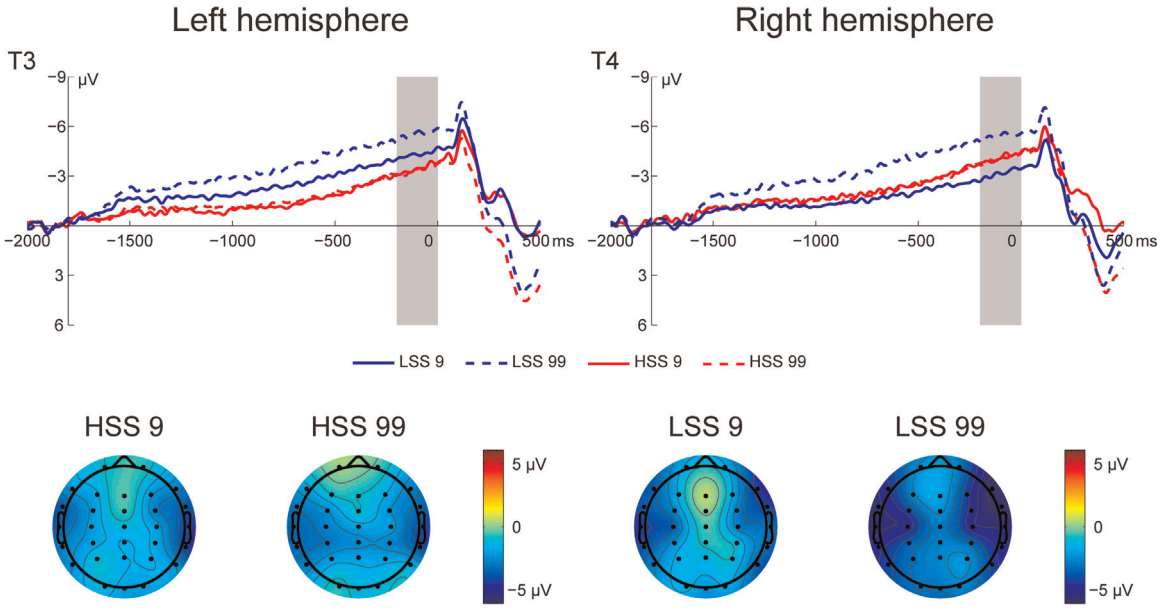

Fig. 3. Grand average ERP waveforms following low- and high-risk decisions for high sensation seekers (HSS) and low sensation seekers (LSS) at T3 and T4, where the shaded areas depict the time window of the stimulus-preceding negativity (SPN). Topographic maps of the SPN (−200 to 0 ms) are also shown.

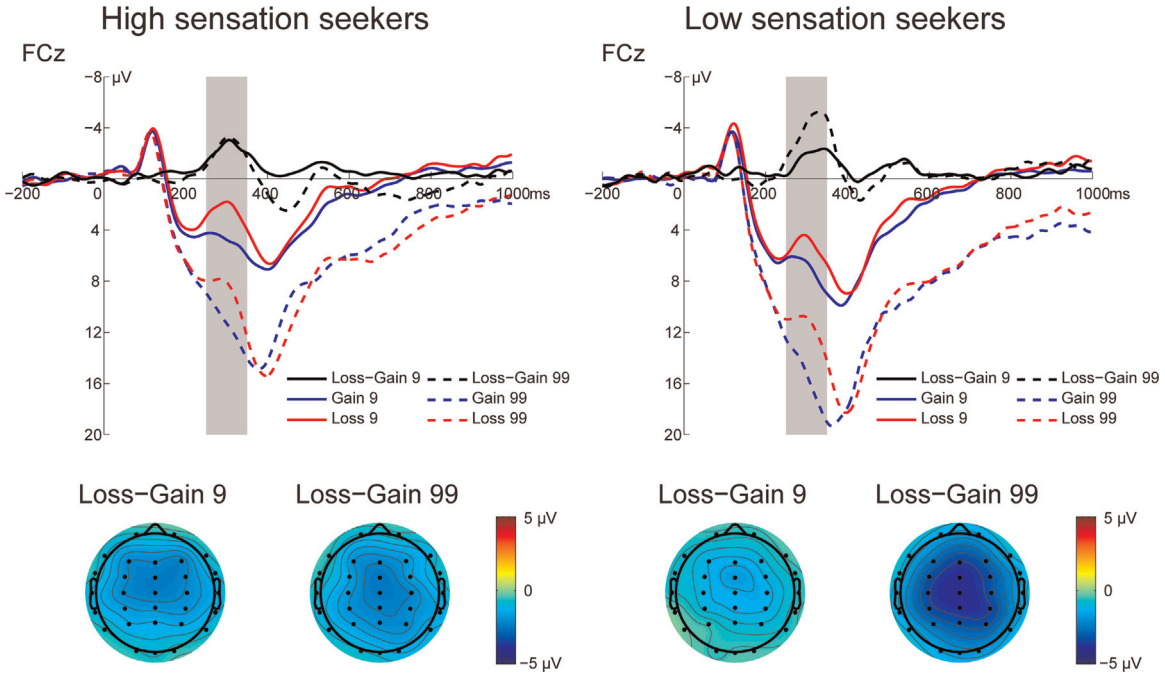

Fig. 4. Grand average ERP waveforms for gains and losses by risk and sensation seeking at FCz. FRN (calculated as the difference between loss and gain waveforms) for low- and high-risk outcomes is shown with shaded areas depicting its time window. Scalp maps (250–350 ms) show the topography for the FRN by risk and sensation seeking.

immediately prior to the feedback onset. Moreover, the SPN appeared to be more pronounced at lateral electrode sites. The SPN was larger following high-risk choices compared to following low-risk choices for LSS, but showed no effect of risk for HSS, as revealed by a significant interaction between group and risk (Fig. 2D), $F(1, 41)=4.86$, $p=.033$, $\eta_p^2=.11$.

3.2.2. FRN

Fig. 4 presents topographic maps for HSS and LSS depicting voltage differences across the scalp for FRN from 250 to 350 ms after the feedback onset. Grand average ERP waveforms at FCz elicited by gains and losses and difference waveforms (losses minus gains) are also presented in Fig. 4. Across the groups, the FRN was observed as a frontally maximal ERP component peaking at approximately 300 ms. High-risk outcomes elicited a more pronounced FRN than low-risk outcomes did, as reflected by a significant main effect of risk, $F(1, 41)=5.82$, $p=.020$, $\eta_p^2=.12$. Critically, this risk effect was strongly qualified by a significant interaction between group and risk (Fig. 2E), $F(1, 41)=5.13$, $p=.029$, $\eta_p^2=.11$. For HSS, the FRN amplitude following low-risk

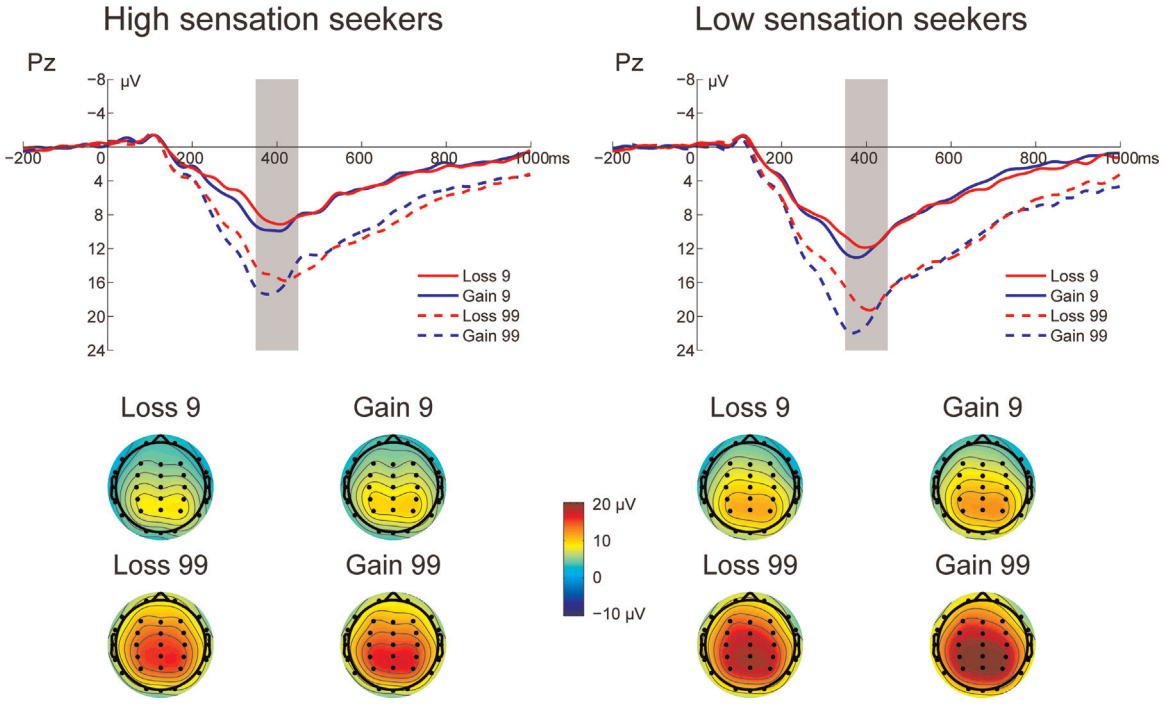

Fig. 5. Grand average ERP waveforms for gains and losses by risk and sensation seeking at Pz, where shaded areas depicts the P300 time window. Scalp maps (350–450 ms) show the topography for the P300 by risk and sensation seeking.

outcomes and high-risk outcomes was comparable ($p=.918$). For LSS, however, the FRN amplitude elicited by high-risk outcomes was significantly more negative than that elicited by low-risk outcomes ($p=.002$).

3.2.3. P300

Grand average ERP waveforms at Pz elicited by gains and losses are presented in Fig. 5. The topographic maps for P300, from 350 to 450 ms, are also shown in Fig. 5. There was a significant main effect of risk, $F(1, 41)=159.72$, $p<.000001$, $\eta_p^2=.80$, with a larger P300 following high-risk versus low-risk outcomes. The P300 was also enhanced for gains compared to losses, reflected in a significant main effect of valence, $F(1, 41)=16.61$, $p<.001$, $\eta_p^2=.29$. Importantly, there was a significant main effect of group, $F(1, 41)=4.43$, $p=.042$, $\eta_p^2=.09$, indicating that the P300 was reduced for HSS as compared to LSS (Fig. 2F).

3.2.4. Repetition effect

Since sensation seeking is associated with fast habituation (Zuckerman, 1990), we reanalyzed the ERP data (see Supplementary Materials) to investigate whether repetition might explain the ERP effects obtained above. The results revealed that the SPN and FRN findings in sensation seeking (i.e., the significant interaction between risk and group) were not affected by repetition. However, the P300 finding (i.e., the group effect) was modulated by repetition such that the group effect appeared in the second but not in the first half.

4. Discussion

The present study investigated the electrophysiological correlates of reward processing in sensation seeking with a risky decision-making task. Our findings indicated that sensation seeking modulated the effect of risk (magnitude of gain/loss) on behavioral choice, with LSS being more risk averse at higher magnitude and HSS showing no change to different risk levels. In addition, HSS and LSS did not differ in their overall task engagement, which was supported by the following observations. First, the decision-making time was similar between HSS and LSS. Second, conditional analysis revealed that the risk preference was similarly influenced by the outcome on the previous trial across the two groups. More importantly, the risk effect on behavioral choice in sensation seeking was consistently reflected by the neural signals from the reward anticipation stage as indexed by the SPN to the outcome-appraisal stage as indexed by the FRN and P300. These findings provide insights into the mechanism underlying risk-taking behavior in sensation seeking.

To our knowledge, this is the first study to examine the neural activity of anticipation in sensation seeking. The SPN was enhanced after high-risk relative to low-risk decisions, which accords with previous research (Mattox et al., 2006; Poli et al., 2007). However, the SPN risk effect appeared among LSS who exhibited a risk-averse pattern, but disappeared among HSS who displayed a risk-neutral pattern. The SPN finding extends our recent study finding that the effect of risk on the SPN appeared when people were risk averse in a gain context but disappeared when the people were risk neutral in a loss context (Zheng et al., 2015). The SPN has been thought as an electrophysiological index of anticipatory, dopaminergically mediated activity (Brunia et al., 2011). In most previous SPN studies, participants performed a time-estimation task where they did not know whether they would receive positive or negative feedback (Chwilla and Brunia, 1991; Kotani et al., 2001; Ohgami et al., 2004), and thus it was unclear that whether the SPN was associated with reward anticipation or loss anticipation. In contrast, the SPN in the gambling task here might index the anticipation of receiving a reward feedback. Presumably, when making a decision between two options, participants would choose the option that they believed to have a higher likelihood to win, even though they did not know the outcome in advance. Of course, future research manipulating the valence of anticipation directly is needed to determine whether the gain anticipation or the loss anticipation is impaired in sensation seeking.

Interestingly, HSS's reduced response to risk during the anticipation stage extended to the outcome-appraisal stage. The FRN amplitude, when calculated as the difference between losses and gains, was enhanced following high-risk compared to low-risk choices. Critically, this risk effect on the FRN only appeared for LSS but disappeared for HSS. Although high risk-taking tendency in sensation seeking is a well-known phenomenon (Zuckerman, 2007), the present study provides the first evidence that the reduced risk effect in HSS emerges at the very early stage (within 300 ms) of the outcome-appraisal. In consistence with our findings, previous studies found that the FRN was comparable between high- and low-risk outcomes among people who were more willing to take risk (Polezzi et al., 2010; Zheng et al., 2015). Recent research, using the same difference measure of the FRN, has associated the variation in the FRN amplitude with both subjective and behavioral indices of reward sensitivity (Carlson et al., 2011; Foti et al., 2011) and suggested that this component actually reflects a reward positivity (Holroyd, Pakzad-Vaezi, and Krigolson, 2008; Proudfit, 2015). Therefore, this blunted risk effect on the FRN may be driven by reduced motivational significance in sensation seeking (Gehring and Willoughby, 2002; Yeung et al., 2005).

At the relatively late stage of outcome-appraisal, the P300 amplitudes in response to gain and loss outcomes were reduced for HSS compared to LSS, indicating that sensation seeking affected the in-depth processing of positive and negative rewards. The P300 is thought to reflect the allocation of attentional resources involved in stimulus evaluation based on motivational significance (Donchin and Coles, 1988; Nieuwenhuis et al., 2005). The reduced P300 for losses is supportive of a hypoactive avoidance system in sensation seeking, which is evidenced by a reduced brain activation to punishment (Kruschwitz et al., 2012) or the absence of reward (Cservenka et al., 2012) among individuals with high sensation seeking. However, the reduced P300 for positive rewards appeared unexpected, as previous research found that sensation seeking was associated with an enhanced activation to rewards (Kruschwitz et al., 2012) and an enhanced sensitivity to the reinforcing effect of psychostimulant drug (Kelly et al., 2006; Stoops et al., 2007). Interestingly, the group effect on the P300 was a function of task repetition such that HSS displayed a habituation effect compared to LSS, which is consistent with previous research (Zuckerman, 1990).

Overall, the blunted neural responses to monetary risk in sensation seeking may be interpreted with the optimal arousal theory (Zuckerman, 1969, 1984). According to this theory, sensation-seeking behaviors are attributable to individual differences in an organism's optimal arousal level and that any departure from the optimal level would cause approach or avoidance for stimulation. Generally, HSS compared to LSS have a higher level of optimal arousal and thus need more novel and intense sensation to reach the higher optimal level. Therefore, a level of stimulation preferred by LSS may fail to reach the optimal arousal level for HSS, which explains the reduced risk effect on neural responses among HSS in the anticipation stage and in the outcome-appraisal stage. In other words, HSS compared to LSS may have a hypoactive brain system, and consequently, they need higher stakes to perceive differences in riskiness. In real life, people high on sensation seeking tend to seek more intense sensation to reach an optimal level of arousal by taking risks.

Our ERP data lend some support to the motivational theory

(Joseph et al., 2009; Lissek et al., 2005). The reduced P300 for loss outcomes in HSS compared to LSS is consistent with a hypoactive avoidance system in sensation seeking. For instance, recent research found that sensation seeking was associated with a deficient brain response to monetary punishment (Kruschwitz et al., 2012), a reduced negative bias (Zheng et al., 2011), a blunted response when making an error (Santesso and Segalowitz, 2009; Zheng et al., 2014), and a reduced autonomic response in the face of emotionally negative stimuli (Lissek et al., 2005; Lissek and Powers, 2003).

However, our findings are at variance with the hypothesis of a hyperactive approach system in sensation seeking, which is evidenced by enhanced brain activation for positive stimuli in individuals with high sensation seeking (Joseph et al., 2009; Kruschwitz et al., 2012). On the contrary, it is tempting to suggest that sensation seeking falls under the rubric of reward deficiency syndrome (RDS), a theory suggesting that a dysfunctional state in the "brain reward cascade", especially in the dopaminergic system, causes a sluggish motivational system (Blum et al., 1996; Comings and Blum, 2000). Indeed, sensation seeking, albeit inconsistently, has been linked to a dysfunctional dopaminergic system (Derringer et al., 2010; Gjedde et al., 2010). For example, novelty seeking, a trait highly correlated with sensation seeking, was predicted by reduced dopamine D2/3 receptor availability in the ventral tegmental area and substantia nigra (Zald et al., 2008) and in the right insular cortex (Suhara et al., 2001). However, the RDS hypothesis in sensation seeking is speculative and future research should address it more directly.

One limitation of the current study concerns the modest sample size (21 HSS and 22 LSS) and our use of a sample consisting of college students, although most of the existing sensation-seeking studies have recruited college students as participants. Even though sensation seeking is a strong predictor of risk-taking behaviors (Zuckerman, 2007), participant recruitment and grouping base on a single personality questionnaire limits the generalizability of our findings. Therefore, it is of great importance to include ecologically valid sample (e.g., sky-divers) as HSS in future research, so as to compare the "real-life" HSS with the scored HSS for the validation of the sensation-seeking trait.

In summary, our findings revealed that risk-taking behaviors in sensation seeking were consistently reflected in the anticipation stage and in the outcome-appraisal stage. HSS were risk neutral in a risky decision-making task. Similarly, they showed no effect of risk on the SPN and FRN. Moreover, HSS displayed a blunted P300 to both the gain and loss outcomes. These findings are thus more supportive of the optimal arousal theory than the motivational theory. As a valid predictor of substance use, sensation seeking has been a potential target for addiction prevention (Everett and Palmgreen, 1995; Perry et al., 2011; Sargent et al., 2010). Our data thus provide tentative evidence of a diminished risk processing in high-risk individuals for addiction and future research should address directly the effect of sensation seeking on the reward system associated with addiction.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2015.04.002.

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