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Nothing to lose: Processing blindness to potential losses drives thrill and adventure seekers

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Abstract

Sensation seeking has been linked to increased risk taking and is therefore crucial in influencing behavioral outcomes of risk-taking behavior. Using functional magnetic resonance imaging (fMRI), the neural underpinnings of risk appraisal were studied in a large subject sample (n=188), stratified according to thrill and adventure seeking (TAS) ratings. As defined by a median split of the sample, low and high TAS groups were compared on a simple decision-making task completed during fMRI. The task was designed such that risk (i.e., magnitude of outcome) and gains (i.e., direction of outcome) could be mapped independently. Behavioral analysis indicated that high TAS individuals are more sensitive to rewards but less discriminating between risk with and without punishment and that low TAS individuals are less sensitive to rewards but quite sensitive to receiving punishments in risky situations. Imaging results on the group differences for the interaction between level of risk and level of gain showed differences in the right superior frontal gyrus (BA6), left insula (BA21), right nucleus accumbens, left lentiform nucleus, and left precuneus (BA7). The presented data suggest a neural model of risk processing in sensation seeking individuals such that the positive response to reward outweighs the impact of equivalent loss. This imbalance in approach/avoidance is evident in differences in the underlying neural substrates in TAS individuals and leads to greater risk behavior in the face of potential loss.

Keywords

sensation seeking; fMRI; SFG; neural correlates; decision making; risk taking

1. Introduction

Decision-making is an important function of everyday life in which we are faced with choices when the outcomes are unpredictable and incur a significant risk. Broadly, decision-

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making can be defined as selecting an action from a set of available options that may result in an outcome that leads to a change in the psychological and physiological state of the decision-maker (Paulus, 2007). A pivotal part of decision-making is the evaluation of level of risk (defined in a later section) that helps to decide whether to approach or avoid certain situations. Thus, individuals must be able to evaluate their current needs according to their current psychological and physiological states, as well as to the environmental conditions. Decision-making can be modeled as part of a homeostatic process (Paulus, 2007) in which decisions maintain or bring individuals into a new homeostatic state. Several investigators have suggested that it is different baseline arousal levels which motivate individuals to avoid or seek sensations with the aim to maintain an optimal or homeostatic level of arousal (Zuckerman et al., 1980).

Sensation seeking is a personality trait defined as seeking of varied, novel, complex, and intense sensations and experiences, and the willingness to take physical, social, legal, and financial risks for the sake of such experience (Zuckerman, 1994, p.27). Sensation seeking in turn is comprised of several facets: thrill and adventure seeking, experience seeking, boredom susceptibility, and disinhibition (Zuckerman, Eysenck & Eysenck, 1978). Individuals with high sensation seeking scores and, in particular, high thrill and adventure seeking (TAS) engage more frequently in high- physical impact and high-risk sports such as rock-climbing, scuba diving and hang-gliding (Roberti, 2004; Zuckerman, 1994). Given that arousal differs with the amount of experienced stimulation and with the perceived riskiness of a situation, cognitive and physiological arousal would be expected to increase with stressor intensity (Noteboom et al, 2001). Consistent with this notion, there are well-known differences between high and low sensation seekers (SSs) in autonomic response patterns and cortical arousal in response to intense visual or auditory stimuli (especially at high-intensity levels). Pascalis et al. (2006) used their findings in autonomic patterns to suggest that high impulsive-SSs are more arousable and less prone to defensive reactions to novel or aversive stimulation. Brocke et al. (1998) replicated and extended on prior research by using EEG to show a correlation between TAS and cortical arousal, suggesting that high TAS individuals, relative to low TAS individuals, show a greater neural response to intense auditory stimuli. Taken together, it appears that high sensation seekers show hypersensitivity to intense stimuli, but reduced sensitivity to aversive stimuli (Joseph et al., 2009). This notion was implemented in Zuckerman's model of sensation seeking (1994), which assumes that high sensation seekers produce strong approach and weak avoidance reactions in response to novel situations that include possibilities of primary reward and punishment (Lang et al, 2005). From this it follows that high sensation seekers relative to low sensation seeking individuals would obtain distinct homeostatic evaluation processes that subsequently result in differences in approach and avoidance behavior of certain situations – i.e., influencing decision-making or taking a risk.

As activities to achieve the preferred level of arousal differ in their riskiness (Zuckerman, 1994), risk taking is a behavioral correlate of sensation seeking but would not be a primary motive in behavior (Zuckerman, 1994). Operationally, risk-taking can be defined as the propensity to select an action with the potential for a relatively large beneficial or adverse outcome over an alternative action that results in a relatively small beneficial or small adverse outcome (Slovic, 1987, Mellers et al., 1997, Paulus et al., 2003). Based on the notion that risk is fundamentally subjective (Slovic, 1992), high sensation seekers relative to low sensation seekers do not differentially perceive engaging in risky behaviors as being risky, threatening, and having negative consequences (Roberti, 2004; Zuckerman, 1994). Thus, high sensation seekers may be more likely to repeat and engage in activities that encompass objectively increased risk (Horvath & Zuckerman, 1993). It can be assumed, then, that high TAS individuals relative to low TAS individuals would exhibit more motivation to select responses that are associated with higher risks (i.e. +/- 80 in the "risky gains task" used in

this study). Given that risk perception evolves depending on outcome - e.g. loss or punishment - (Cohen et al., 2008), it can be suggested that risk perception following punishment would change differently for low and high TASs based on Zuckerman's model of sensation seeking (1994).

Whereas much is known about the differences in autonomic response pattern as well as risk-taking and its relationship to sensation seeking and various personality characteristics, much less is known about the neural processes that underlie these differences. Using low and high arousing pictures in a functional magnetic resonance imaging (fMRI) study, Joseph et al. (2009) characterized the neurobiological profile of emotional arousal and reactivity in SS. In particular, fMRI responses to high-arousal stimuli were stronger in high SSs than in low SSs in the insula. Other fMRI studies have also pointed towards insula activity and its relation to personality characteristics like neuroticism, harm avoidance (Paulus et al., 2003), novelty seeking (Suhara et al., 2001) and anxiety proneness (Simmons et al., 2006) leading to the homeostatic notion that activation in this region may reflect sympathetic states that differ as a function of personality (Paulus et al., 2003). Therefore insula activation may serve as an important neural substrate to instantiate aversive somatic markers that guide risk-taking behavior (Paulus et al., 2003).

In another fMRI study, Abler et al. (2006) found that nucleus accumbens activity was correlated with individual differences in sensation and novelty seeking, indicating a link between the dopamine system and personality traits. In addition, Matthews et al. (2004) found nucleus accumbens activation positively correlated with harm avoidance during risk taking, affirming a connection to personality and temperamental characteristics. In addition to its relationship with personality traits, it has been shown that the nucleus accumbens is critically involved in the anticipation and processing of rewards (Knutson et al., 2001; Abler et al., 2006), as well as essential in taking a risk (Matthews et al., 2004). As the reviewed literature suggests an important link between these structures (i.e., insular cortex and striatal system) and personality characteristics, we propose these "target areas/systems" to relate to risk taking and decision making in combination with differences in sensation seeking.

Another candidate system that may be in a network responsive to TAS risk-based decision-making is the medial frontal cortex. This region has been implicated in conflict monitoring (Botvinick et al., 1999; Carter et al., 1998; Garavan et al., 2003; Ullsperger and von Cramon, 2001), the control of voluntary action (Thaler et al., 1995; Lau et al., 2004; Nachev et al., 2007), risk taking (Paulus et al., 2003; Matthews et al., 2004), as well as the correlation of personality to regional cerebral blood flow (rCBF) (Sugiura et al., 2000). Lesions to this frontal area effect important decision making capacities such as set-shifting (Manes et al., 2002) and inhibition (Floden and Stuss, 2006).

This fMRI study aimed to assess the neural processing differences between high and low TAS individuals during a parametrically graded risky decision-making task. Specifically, we chose to examine the relationship between risk-processing and level of TAS, due to its direct relationship with approach/avoidance in situations of increased risk (e.g., potentially dangerous physical consequences). Furthermore we chose to focus on this specific subscale of the sensation seeking scale form-V (SSS-V) (Zuckerman et al., 1978) as distinct forms of gambling would be differentially related to sensation seeking and its subscales (Breen & Zuckerman, 1999; Fortune & Goodie, 2010), which may result in partly inconclusive results when examining just the total score. To that end, we used the "risky gains task" (RGT), which had been developed to probe the neural circuitry underlying risk-taking decision-making (Paulus et al., 2003). As a construct of TAS comprises the seeking out of increasing levels of intensity, the RGT seems to meet the demands (at least in part) of TAS and its measurement as it includes increasing levels of risk intensities as well as an element of time

pressure. Subjects must act quickly within certain “windows of opportunity” when deciding to accept a safe bet or to pass it up for a bigger risk – i.e. increasing reward but possibility of a correspondingly large penalty (Leland & Paulus, 2005). As TAS activities described in the SSS-V mostly require fast decisions on whether to make an action or not and are then followed by success or correspondingly failure and punishment, the RGT can provide this crucial TAS component.

Based on prior literature we hypothesized first, that high TAS individuals would be more sensitive to rewards and less sensitive to punishments in the RGT than low TAS individuals, which would result in less safe seeking immediately following punishment. Second, the high TAS group would show greater neural sensitivity in response to reward situations and less neural sensitivity in response to punishment situations than low TAS individuals. Third, differences between groups in neural activation patterns in response to gains vs. losses would be correlated with the behavioral outcomes, specifically in the striatum, insula, and medial frontal cortex. Confirmation of these hypotheses would provide the first direct indication of the differences in the neural substrates of thrill seeking individuals while decision-making and could potentially help add to the neural models of risk taking.

2. Methods

2.1. Subjects

188 healthy, right-handed subjects (94 females and 94 males) age 20.73 ± 1.6 with an average education level of 14.39 ± 1.23 years, without any current dependence (except nicotine dependence), and any current Axis I DSM- IV diagnosis participated in this study. Additional exclusion criteria included the presence of unremovable metal, pregnancy and any diagnosed neurological disorder. All subjects completed the Sensation Seeking Scale Form-V (Zuckerman et al., 1978), the NEO Five Factor Inventory (NEO-FFI; Costa and McCrae, 1992), and the Barratt Impulsivity Scale BIS- 11 (Patton et al., 1995) (n = 3 missing).

Subjects were divided (median split of TAS scores) into a low TAS group (N = 94; 47 males; 47 females) and a high TAS group (N = 94; 47 males; 47 females) with significant differences in the TAS score (low TAS = 5.986; high TAS = 9.436; $p < 0.001$). According to the psychometric properties of the SSS-V (Zuckerman, 1978), mean scores of high and low TASs in this study respectively fall within the range of $M \pm SD$ of the Zuckerman (1978) sample. Therefore the range of TAS scores entailed in our sample can be considered to be “normal” for representing *high* vs. *low* TAS characteristics. A correlational analysis was used to determine the relationship between personality measures and behavioral variables (Table 1). Group statistic variables such as gender, age, race/ethnicity, years of education and total number of lifetime uses of drugs are shown in Table 1.

Subjects were taking part in a longitudinal follow up study aimed to examine the development of stimulant use related problems, which was approved by the University of California San Diego Institutional Review Board.

2.2. Task

During the Risky-Gains Task, subjects are presented with three numbers in ascending order (20, 40, and 80). Each number is presented on the screen for one second and if the subject presses a button when the number is shown on the screen, he/she receives the number of points in cents (+20; +40; +80). When a 40 or 80 appears, however, there is a chance that it will appear in red color, along with immediate negative feedback signaling a loss of 40 or 80 cents (−40; −80), respectively. When this occurs, the trial ends immediately (i.e. the subject may not make a response). The subjects are informed prior to performing the task that

waiting to select a 40 or 80 allows for larger monetary gains but risks losing money, while selecting a 20 offers less money but carries no risk of penalty. Unknown to the subject, the probabilities of presenting a negative 40 or 80 are set such that the total amount of cash earned would be identical if they were to consistently select 20, 40, or 80. Thus, there is no inherent advantage to select the risky response (40 or 80) over the safe response (20). Each trial lasts 3.5 s irrespective of the subject's choice and the subject receives rewarding feedback (stimulus on the screen and auditory sound) immediately after selecting a response. Across the task there are 6 occurrences of resting trials (3.5 seconds each). The 96 trials of the Risky-Gains task consist of three trial types, which were presented in randomized order: (1) a non-punished trial type ($n=54$), (2) a punished-negative 40 trial type ($n=24$), and (3) a punished-negative 80 trial type ($n=18$). Actual punishment occurs only if the subject holds out long enough for one to occur, so if a response is made during the 20 window of a negative 40 trial or the 20 or 40 window of a negative 80 trial, the result is the same as if it were an unpunished trial. If, on the other hand, a subject plans to hold out for an 80 on a negative 40 trial, punishment arrives immediately after the 1-s window for a 20 response elapses, just as if he or she planned to choose a 40 or had not yet decided when to respond. Subjects are informed that they will be paid-off with the amount of money earned during the RGT.

2.3. Behavioral measures

The dependent measure in the RGT is response frequency. The main indices of risk-taking are the relative frequency of "safe" responses (20) versus "risky" responses overall (+40; -40; +80; -80) and as a function of previous trial outcome (i.e. unpunished versus punished). The former provides a baseline assessment of risk-taking while the latter probes sensitivity to punishment. To investigate whether outcomes influenced later responses (also beyond just the subsequent trial), a mutual information analysis (described in the statistical analysis section) was performed to assess the degree to which action-outcomes (i.e. selecting 20, selecting 40, selecting 80, being punished) for one trial were related to those for earlier trials at each lag between 1 and 10 previous trials. Another measure of interest is the intended frequency (IF, described in the statistical analysis section) of each choice.

2.4. Procedure

After consenting to the study subjects participated in two sessions. The first session contained a diagnostic assessment based on the SSAGA-II (Semi-Structured Assessment for the Genetics of Alcoholism; Buchholz et al., 1994) and various laboratory tests (i.e. drug – screening urine test). Subjects were asked to complete the inventories of personality questionnaires at home. In the second session subjects were familiarized on a laptop computer with the decision-making task and subsequently completed the task during the fMRI scan. Before leaving, subjects were debriefed and were paid for their participation and the amount of money won in the RGT.

2.5. Functional magnetic resonance imaging

The blood oxygen level dependent (BOLD) fMRI data were collected during the task using a Signa EXCITE 3.0 Tesla-GE scanner (T2*-weighted echo planar imaging (EPI) scans, TR = 2000ms, TE = 32 ms, FOV = $230 \times 230 \text{ mm}^2$, 64×64 matrix, thirty 2.6 mm axial slices with a 1.4 mm gap, 256 whole-brain acquisitions). For anatomical reference, a high-resolution T1-weighted image (spoiled gradient recalled (SPGR), TI = 450, TR = 8 ms, TE = 3ms, FOV = $250 \times 250 \text{ mm}^2$, flip angle = 12° , 176 sagittally acquired slices $1 \times 0.97 \times 0.97 \text{ mm}^3$ voxels) was obtained during the same session.

2.6. fMRI analysis pathway

The data were preprocessed and analyzed with the software AFNI (Cox, 1995). The echo-planar images were realigned to the 128th acquired scan and time corrected for slice acquisition order. To exclude the voxels showing an artifact related to signal drop, a combined threshold/cluster-growing algorithm was applied to the mean of the functional images to compute a cortical- whole brain mask. This screened out non-brain voxels and voxels falling within the artifact region. A randomized fast-event related design was used with 6 resting trials interspersed between the 96 risky-gains trials. The preprocessed time series data for each individual were analyzed using a multiple regression model in which the five regressors of interest were constructed from the behavioral data obtained from each subject. Each regressor function was defined as “on” from the onset of the trial until the subject had made a response or until the subject was presented with a loss of 40 or 80. These five regressors are referred to as (1) selecting 20 (safe response) (2) selecting 40 (risky response); (3) selecting 80 (risky response); (4) punished with -40 (punished risky); and (5) punished with -80 (punished risky). As each regressor models a specific subset of the selection/choice interval, orthogonality of the model is provided. The resting trials (interspersed in 6 occurrences of 3.5 seconds each) and the inter-trial intervals (from the time the subject makes a response to the beginning of the next trial) served as the baseline condition for this analysis. The regressors of interest were convolved with a modified gamma variate function modeling a prototypical hemodynamic response (Boynton et al., 1996) prior to inclusion in the regression model. In addition three regressors were used to account for residual motion (in the roll, pitch, and yaw direction). Regressors for linear trends were used to eliminate slow signal drifts. The AFNI program 3d Deconvolve was used to calculate the estimated voxel-wise response amplitude. A Gaussian filter with FWHM 6 mm was applied to the voxel-wise percent signal change data to account for individual variations of the anatomical landmarks. Data of each subject were normalized to Talairach coordinates. Data was converted into percent signal change by dividing the signal for the regressors of interest by the baseline signal.

2.7. Statistical analysis

The voxel-wise percent signal change data were entered into a linear mixed effects model (LME) with group (low TAS vs. high TAS) as a between-subjects factor and risk (40 vs. 80) and gain (win vs. loss) as within-subject factors to determine ROIs with significant interaction effects on these factors. Whole brain data was clustered to account for multiple comparisons. Data was thresholded at $p < .01$ and clusters were retained that exceeded 1024 μl volume for continuous voxels based on monte-carlo simulations using the AFNI function AlphaSim. We calculated the percent signal change difference for the conditions (win: $|+80 \text{ to } +40| = \Delta+$; loss: $|-80 \text{ to } -40| = \Delta-$) of the RGT for the areas that emerged from the LME and subsequently evaluated BOLD differences between groups within these areas (2 contrasts: $\Delta+$ high TAS vs. $\Delta+$ low TAS; $\Delta-$ high TAS vs. $\Delta-$ low TAS). A correlational analysis was used to determine the degree to which changes in behavior (“safe” baseline vs. “safe” prior punishment) were associated with the amount of change of the BOLD signal when winning or losing in the two risk levels ($+40 \text{ vs. } -40 = \Delta 40$; $+80 \text{ vs. } -80 = \Delta 80$) of the RGT conditions. The relative frequency of drug use was subjected to a multiple linear regression to assure that the task outcome in both groups was not influenced by those possible covariates.

All analyses for the behavioral data were carried out with SPSS 16.0 (Norusis, 2007). A repeated measures general linear model (GLM) was used to analyze the task measure with group as between-subjects factor and response type (risky vs. safe) and previous trial outcome (punished vs. safe) as within-subject factors. Moreover, we performed a 2×2 repeated measures ANOVA with safe and risky responses in baseline vs. prior punishment

conditions as within-subject factors for each group separately accounting for bonferroni adjustments (4 comparisons).

Furthermore, we used three different theoretically derived methods for modeling the behavior. First, we created a measure to determine the “*intended frequency*” (*IF*) of the choice to respond with 80 (i.e. the intention to make a 80 response irrespective of prior punishment or baseline; where we accounted for the uncertainty component of -40 that includes the possible intention of the subject to select 80; $IF\ 80: \text{number \# of 80 responses} + -80\# + (80\#/(40\# + 80\#)) \times -40\#$). Second, using *Shannon entropy* $h = \sum p_i \times \log_2 p_i$ (Shannon and Weaver, 1949) we calculated values to obtain differences in the predictability of behavior between low and high TAS individuals after a punished “risk” 80 was experienced.

Third, using a *mutual information (MI) analysis*, the degree of non-randomness in sequences of action-outcomes was assessed to determine whether participants delivered responses that were influenced by the outcome of the immediately preceding trial and those of up to 10 trials ago. Mutual information functions (Herzel and Grosse, 1995) are based on the logarithmic likelihood ratio between the observed frequency of an event and the expected frequency of an event. These functions quantify, in units of bits, how much more or less likely than chance it is that two events will co-occur, in this case with 0 bits representing complete independence and 1 bit representing perfect prediction of each event by the other. In the RGT, the mutual information will measure the degree to which trials are dependent of each other. In case of dependence of two following trials, the dependent measures “prior punishment” vs. “no prior punishment” would be a valid indicator of sensitivity to punishment. Mutual information was calculated for action-outcomes at separations of between 1 and 10 lags and compared between low and high TAS individuals.

3. Results

3.1. Psychological variables

The two groups showed significant differences in the TAS score (low TAS = 5.986; high TAS = 9.436; $p < 0.001$, the SS total score (low TAS = 21.554; high TAS = 26.343; $p < 0.001$) and in the experience seeking score (low TAS = 5.80; high TAS = 6.60; $p < 0.01$), while other SS subscales did not differ significantly. Furthermore, low and high TASs differed in the NEO subscales extraversion and openness, and these measures were not correlated with the dependent variables. Moreover groups did not differ in their neuroticism score (which was also not significantly correlated with the dependent measures) which is known to be associated with sensitivity to negative stimuli and therefore may result in reduced risk-taking propensity (Paulus, 2003).

3.2. Behavioral data

When use of drugs was entered into a step-wise regression model with the frequency of risky responses (prior punishment) as the dependent variable, no significant model emerged when including all 188 subjects, nor when processed for each single group individually.

GLM—As seen in Fig. 1, there were no significant differences in the risky responses between the prior punishment and baseline conditions ($F(1,93) = 0.077$, $p = 0.782$) nor in the safe responses between the prior punishment and baseline conditions ($F(1,93) = 0.069$, $p = 0.794$) in high TAS individuals. Contrariwise, low TAS individuals showed a significant decrease in risky responses ($F(1,93) = 8.53$, $p = 0.016$, partial $\eta^2 = 0.084$) following a punished trial compared to risky responses with no punishment and a significant increase in safe responses ($F(1,93) = 8.52$, $p = 0.016$, partial $\eta^2 = 0.084$) when previous punishment

occurred. Focusing on risky responses in the “prior punishment” condition, low and high TAS individuals showed significant differences in their response frequency (low TAS = 0.43, high TAS = 0.53, $p = 0.025$), whereas the two groups showed no significant differences in risky responses in conditions without punishment (low TAS = 0.50, high TAS = 0.53, $p = 0.266$) – interaction effect IE group*response type*previous trial outcome $F(1,186) = 3.803$, $p = 0.053$, partial $\eta^2 = 0.02$. Furthermore, low TAS individuals made significantly more safe responses than high TAS individuals (IE group*response type: $F(1,186) = 3.814$, $p = 0.052$, partial $\eta^2 = 0.02$). Moreover, we observed an IE of previous trial outcome and response type ($F(1,186) = 5.375$, $p = 0.022$, $\eta^2 = 0.028$), whereas additional effects were not observable (main effect (ME) group: $F(1,186) = 3.066$, $p = 0.082$, $\eta^2 = 0.016$; ME previous trial outcome: $F(1,186) = 3.066$, $p = 0.082$, $\eta^2 = 0.016$; ME response type: $F(1,186) < 0$, $p = 0.819$; IE group*previous trial outcome: $F(1,186) = 3.066$, $p = 0.082$, $\eta^2 = 0.016$).

IF—Low TASs differed from high TASs significantly in the intended frequency of making a risky 80 choice (low TASs = 0.22, high TASs 0.26, $p = 0.046$).

Shannon entropy—The calculated entropies for both groups as a result of an experienced punished 80 trial are shown in figure 2. A significant quadratic interaction between the groups and level of risk (“safe” 20, “risk” 40 and 80) in the RGT was found ($F(1, 186) = 7.206$, $p = 0.008$, partial $\eta^2 = 0.037$) containing a significant difference in the entropy of the 40 condition between low and high TAS individuals (low TAS: 1.38; high TAS: 1.56; $p = 0.02$).

MI—Low TAS individuals did not differ significantly from high TAS individuals in the degree to which action-outcomes were related to those of previous trials at various lags ($F(1, 186) = 0.372$; $p = 0.543$). As the mutual information function resulted in a mean value of 0.43 (0.14 S.D.) for trials of one lag, it can be suggested that subsequent trials are influenced by the previous trial outcome. MI values for two and more lags were significantly smaller (two lags: mean = 0.02; S.D. = 0.03; $p < 0.001$) indicating relative independence of these trial outcomes.

3.3. Neuroimaging data

As shown in table 2, based on the LME (group; risk; gain) with a volume-thresholded cluster of 1024 μ l, thirteen areas showed significant interaction effects. These areas included left precuneus (BA7), left middle temporal gyrus, (BA37), left insula (BA21), left inferior frontal gyrus (BA46), right middle temporal gyrus (BA37), left lentiform nucleus, right nucleus accumbens, right superior frontal gyrus (BA6), left subcallosal gyrus (BA34), right precuneus (BA31), left precentral gyrus (BA6), and left and right superior frontal gyrus (BA8). Figures 3a–3e show activation patterns for right superior frontal gyrus (BA6), left lentiform nucleus, left precuneus (BA7), right nucleus accumbens, and left insula (BA21).

Extracted data were classified in two specific contrasts. First, high TAS individuals show more neural sensitivity to rewards than low TAS individuals ($\Delta + \text{high TAS} > \Delta + \text{low TAS}$). Second, high TAS individuals show less neural sensitivity to punishment intensities than low TAS individuals ($\Delta - \text{high TAS} < \Delta - \text{low TAS}$). Classification of areas regarding these contrasts is shown in table 2.

3.4. Neuroimaging correlations with behavioral responses

We observed that individuals with fewer safe selections after punishment (i.e. high TAS individuals) showed relatively more difference in BOLD activation ($\Delta 80$) when winning (+80) or losing (−80) in the high-risk option. Table 3 shows the specific areas in which this

effect was found. In contrast we didn't observe any expedient correlations for the low risk option (risk 40).

4. Discussion

This study yielded three main findings. First, behaviorally, high relative to low TAS individuals are less sensitive to punishments and engage in more risky behavior after prior punishment. Second, high TAS individuals show greater activation to rewards than low TAS individuals in the right superior frontal gyrus (SFG) (BA6), left insula (BA21), left lentiform nucleus, right nucleus accumbens, and left precuneus (BA7). In comparison, low TAS individuals are more sensitive in evaluating different punishment intensities in risky situations in several key areas including the left SFG (BA6), right nucleus accumbens, and left precuneus (BA7) (Fig. 3a – 3e). Third, there was an association between changes in behavior with the amount of change of BOLD signal when winning (+80) or losing (−80) in areas important for decision-making (right SFG (BA6), left insula (BA21), right nucleus accumbens, left lentiform nucleus, and left precuneus (BA7)) in the high TAS group relative to the low TAS individuals.

Behaviorally we found that low and high TAS individuals showed similar frequencies of “safe” and “risky” responses. However, low TAS but not high TAS subjects selected the safe option more frequently after punishment (figure 1). Given that experience with any activity that does not lead to punishment reduces the risk appraisal of that activity (Zuckerman, 1994), the baseline condition can be interpreted as a “low risk” situation that leads to an equal risk appraisal in low and high TAS individuals, which results in the same response patterns for both groups. It can be suggested that low and high TAS individuals are equally influenced by rewards when there is no punishment, i.e. the prospect of gaining 40 or 80 cents during the RGT, but are not equally influenced by punishments, as only low TAS individuals showed a reduced frequency of risky responses immediately following punishment. Moreover, we found that high TAS individuals intended a “risk 80” response more often than low TAS individuals, even though chasing “risk 80” encompassed increased risk of punishment. This reduced sensitivity to punishment in high TAS individuals is consistent with the general notion of a weakly active avoidance system in high sensation seeking (Zuckerman, 1994).

The right superior frontal gyrus SFG (BA6) may play a significant role in modifying behavior in TAS individuals. Specifically, the degree of BOLD-fMRI signal change to potential large punishments and large rewards in this area showed the highest correlation with subsequent behavior for the high TAS group (table 3). This area is widely considered to be of central importance for the ability to select what action is performed (i.e. pre supplementary motor area - pre-SMA) due to its role in movement initiation and inhibition (Nachev et al., 2007). It has been shown that monitoring processes in the posterior medial frontal cortex (pmFC) engaged in the need for adjustment to achieve action goals cluster in a transition zone which includes BA 6 and is known to be extensively connected to brain areas that take part in controlling cognitive and motor processes (Ridderinkhof et al., 2004). Therefore, it seems that differences in the availability of processing resources for gains and losses in this area may bias behavioral adjustments for low and high TASs differently. Regarding the SFG activation pattern in this current study (figure 3a), it can be suggested that activity in both valence domains (reward vs. punishment) possibly codes magnitude (40 vs. 80) of a potential loss or gain domains dependently. From this it follows that loss of −80 > −40, and win of +80 > +40. Although magnitude seems to be coded domain specific, it can be speculated that the relative difference of the magnitude Δ (win vs. loss) of a risk may be processed in way of a cost-benefit tradeoff, resulting in the preference of a certain action as we found this measure ($\Delta 80$) to be correlated to the subsequent behavior (table 2).

Consistent with this suggestion, there is strong evidence (e.g. Nachev et al. 2005, 2007; Botvinick, 2007; Kounieher et al., 2009) that regions in the MFC (e.g. dorsal anterior cingulate cortex (ACC); pre-SMA) implement cost-benefit tradeoffs for regulating cognitive control resources. Specifically, Kounieher et al. (2009) found that the pre-SMA and the posterior lateral PFC region were involved in contextual control where the current cue was used for selecting task-appropriate behavior, similar to the brain-behavior relationship in the current study. Kounieher and colleagues argue that the pre-SMA assesses current cues of incentives and gauges the costs associated with behavioral selection. Thus, these authors argue that potential benefits are deemed to outweigh associated costs, activating the pre-SMA to engage in contextual control operations (Egner, 2009; Kounieher et al., 2009) and subsequently influence the execution of planned action. Based on this notion, low relative to high TAS individuals exhibit less motivation to select responses that are associated with higher risks (i.e., ± 80), which may allow a balanced processing of both gains and losses. Inversely, high TAS individuals' prospect to potentially gain 80 cents may outweigh the potential costs - resulting in an unbalanced profile ($\Delta 80$) and therefore in "blindness" to potential losses. This speculation (i.e., that "conflict-monitoring" in the SFG (i.e. pre-SMA) is crucially linked to personality characteristics) is furthermore supported by a study of Sugiura et al. (2000), who associated the SFG (-25, -9, 59) with harm avoidance as they found this measure to be negatively correlated to the rCBF (resting state) in this region. As the TAS subscale is negatively correlated with measures of harm avoidance (McCourt et al., 1993) our finding complements the relation of the SFG to personality characteristics.

Interestingly, we found a similar activation pattern, neural sensitivity to rewards (table 2) and correlation of BOLD signal ($\Delta 80$) to changes in behavior (table 3), to that seen in the SFG in both the dorsal striatum (i.e., left lentiform nucleus; figure 3b) and in the left precuneus (figure 3c). Delgado et al. (2003) proposed that the dorsal striatum serves as an integral component of a reward circuitry, serving to code for feedback properties such as valence and magnitude – and would therefore take part in the control of motivated behavior. Due to its extensively afferent and efferent cortical connections (e.g. to the SMA) and the similarity of the observed activation patterns of the dorsal striatum and the right SFG, it may be proposed that valence and magnitude are coded similarly during this decision-making process. Thus, responses of the dorsal striatum - especially the left lentiform nucleus - seem to be directly tied to personality-related differences in cortical and behavioral responses to gains and losses. It has been shown that the precuneus (BA7) obtains extraparietal connections to the dorsal premotor area, the SMA, and ACC (Petrides and Pandya, 1984; Goldman-Rakic, 1988; Cavada and Goldman-Rakic, 1989; Leichnetz, 2001), whereas one major subcortical connection includes the putamen (Leichnetz, 2001). Evidence suggests that the precuneus plays an important role in the supply of decision strategies enabling the subject to form responses that are based on the previous responses and stimuli as well as their associated outcome (Paulus et al., 2001). Following this notion, the similarity of this structure's activation pattern to the activation in the pre-SMA and dorsal striatum seems consistent. As the reviewed literature suggests a conjoint role of these areas - SFG, dorsal striatum, precuneus - (which is further evidenced by the current data), it can be speculated that these areas may play a conjoint key role while performing TAS motivated decisions related to achieving a homeostatic state.

Regarding the nucleus accumbens (figure 3d), we did not find a significant correlation of 80 to safety seeking after punishment for the high TAS group alone. Nevertheless we found this measure to be correlated to the whole sample, which reveals the relative importance of this structure as it relates to risk taking (Matthews et al., 2004) and its involvement in the anticipation and processing of rewards (Knutson et al., 2001; Abler et al., 2006). Based on the idea that risk-taking behavior may be reinforcing (as the anticipation of risky outcomes activates reward-related systems; Matthews et al., 2004), it seems that only the prospect of a

high reward appears reinforcing for high TAS, whereas low TAS experience reinforcement already in prospect of a small reward. This finding contributes to the results of the behavioral data in that high TAS intended to “chase” the risk 80 condition more often than low TAS.

Furthermore we found $\Delta 80$ related activation in the insular cortex to be correlated with behavioral changes in the RGT. Effects presented in this study reside in the posterior insula (figure 3e), which is implicated as the basic receptive area for visceral input encoding physiological states of the body, and therefore is strongly involved in subjective feeling states and interoceptive awareness (Craig 2002, Critchley et al., 2004). Furthermore, the insula is suggested to play an important role in serving as a neural substrate to instantiate aversive somatic markers as a function of personality that in turn would guide risk-taking behavior (Paulus et al., 2003). Following this notion and regarding the activation pattern, we found it could be speculated that somatic markers in the high-risk condition (+80/−80) are biased for both valence domains in low TAS individuals leading to a more balanced profile of avoidance and approach of this situation. In contrast, high TAS individuals show a relatively weak fMRI response to potential losses, but a relatively strong positive activation in prospect of gaining 80 cents. Thus, it could be argued that high vs. low TAS individuals may obtain distinct interoceptive evaluation processes (i.e., altered homeostatic responses) influencing approach and avoidance of certain situations – specifically influencing decision-making and risk-taking. Although Joseph et al. (2009) found that high sensation seekers engaged the anterior insula more strongly in face of intense arousal, our findings in the posterior insula overlap to a considerable degree in that high TAS individuals also obtained higher activation in face of intense stimuli (i.e. high risk). Additionally we show that this distinct activation in low and high TASs can be separated by positive or negative valence of the potential outcome, which also relates to behavioral differences.

Taken together, findings of this study suggest that greater imbalance between allocating processing resources in decision-making circuits to gains vs. losses related to fewer subsequent non-risky responses, i.e. less “safety seeking”. High TAS individuals engage predominantly in reward-driven behavior and may ignore the perils of losses. In contrast, low TAS individuals spend “equal” processing resources when encountering risky gains vs. risky losses and behave more predictably following punishment. As Zuckerman (1994) describes high sensation seeking to be characterized by a lack of inhibition, these results support the notion that low TAS is not a “passive” characteristic but reflects a more “active” processing of both gains and losses. The homeostatic notion of risk-taking may overlap considerably with the construct of sensation seeking such that a homeostatic imbalance in processing of gains vs. losses can be seen as one factor among others that leads to the imbalance of avoidance and approach systems in high sensation seekers or rather high TAS individuals. This imbalance in turn would drive high TAS individuals to achieve their homeostatic equilibrium by further seeking out reward arousal while being insensitive to loss arousal.

This study has several limitations. As the behavioral task utilized in this investigation just includes two levels of increasing risk intensity, we were only able to show behavioral consequences in one (risk “80”) of the two risk conditions. The fact that we didn’t find any expedient correlations in the “risk 40” condition could be due to the simple fact that this reward intensity was too small to induce reward-driven or sensation seeking motivated behavior in high TASs individuals. Alternatively, the low risk option attracts low TAS individuals and therefore helps to dissociate risk level, which then gives meaning to the high risk option. Future research should attempt to utilize tasks with a larger spectrum of risk intensities to be able to characterize reward and loss dependent behavior in SS as well as its underlying neural processes in more detail. Moreover, examining those effects of a less

categorical risk level may provide additional information. Following this approach, future research could examine at which risk-intensity high TAS individuals would reach their homeostatic balance and subsequently would adapt their behavior to punishment. Moreover, it has to be stated that results presented in table 3 are explanatory/post hoc, whereas the respective analysis was performed to probe whether obtained results were more “driven” by individuals in the low or high TAS group. Although correlations with all subjects may suffer from a selection bias, they are presented for completeness. The lack of significant correlations between the difference in BOLD activation ($\Delta 80$) to safety seeking in low TAS individuals, could suggest that further alignment of processing resources of potential losses to gains (beyond a certain ratio of allocation) would primarily lead to loss driven behavior - i.e., beyond a certain degree of alignment, the difference of +80 and -80 would not be correlated to safer seeking after punishment as there would not be enough variance in behavior.

In summary, this study supports the hypothesis that engagement in risky behavior for the sake of intense sensations is moderated by a weak avoidance system and a strongly activated approach-system in sensation seeking, in particular TAS. These two systems appear to engage decision-making circuits differently, specifically in the right SFG (BA6), left dorsal striatum, left precuneus (BA7), right nucleus accumbens, and left insula (BA21). These findings may be helpful for determining neural biomarkers that could be targets for treatments that aim to balance the interoceptive responses to decisions where risk/gain behavior is clinically concerning (i.e., drug abuse, pathological gambling and other addictions).

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Figure 1.

Relative frequency of risky and safe responses made by low and high thrill and adventure seekers in the risky-gains task. “Baseline” trials are those in which no punishment was scheduled to occur, whereas “Prior Punishment” trials are those following punishment from the previous trial. Low thrill and adventure seekers differed significantly (* $p < .05$) from high thrill and adventure seekers in the frequency of risky responses in trials with prior punishment. Error-bars represent standard errors of the mean.

Figure 2. Entropies (Shannon entropy $h = \sum p_i \times \log_2 p_i$ (Shannon, 1949)) of level of risk (“safe” 20, “risk” 40 and 80) in the risky-gains task for low and high thrill and adventure seekers when experienced a punished “risk” 80 condition. Immediately following punishment in the “risk” 80 condition high relative to low thrill and adventure seeker were more likely to chase a risk (40) over again. Thus, low TAS individuals were “more predictable” than high thrill and adventure seeker after punishment in the high risk condition.

Fig. 3a

Figure 3.

a–e Activation patterns of selected areas (3a. right superior frontal gyrus (BA6); 3b. left lentiform nucleus; 3c. left precuneus (BA7); 3d. right nucleus accumbens; 3e. left insula (BA21)) with significant group differences in a whole brain analysis for the interaction between level of risk and level of gain (risky-gains task)) as a result of the LME (table. 2; 1024 μ l volume-thresholded cluster). All areas show a correlation between the relative difference of BOLD signal $\Delta 80$ when winning (+80) or losing (–80) and changes in behavior following punishment (“change to safety behavior”; table. 3). Furthermore, all areas show a significant difference in the contrast $\Delta+$ high TAS > $\Delta+$ low TAS ($\Delta+$ = gains (+40 vs. +80)), whereas the left superior frontal gyrus (BA6), left precuneus (BA7), and right nucleus accumbens show a significant difference in the contrast $\Delta-$ high TAS < $\Delta-$ low TAS ($\Delta-$ = losses (–40 vs. –80)) (table. 2). Error-bars represent standard errors of the mean.

Table 1

Personality measures of SSS-V, BIS, and NEO-FFI compared between low TAS and high TAS groups and correlations between personality measures across group and level of behavioral risk taking during task./Sociodemographics.

Measures	low TAS (n = 94)			high TAS (n = 94)			t-Test	Risky (no prior punishment)	RGT Corr. r
	n	Mean	S.D.	n	Mean	S.D.			
SS	94	21.55	5.31	94	26.34	4.27	<0.001**	0.03	0.202**
Total score	94	5.98	1.83	94	9.43	0.74	<0.001**	0.07	0.189**
Thrill and adventure seeking	94	5.80	2.10	94	6.60	1.74	0.005**	0.02	0.106
Experience seeking	94	6.35	2.51	94	7.01	2.52	0.074	- 0.02	0.109
Disinhibition	94	3.40	1.83	94	3.28	2.19	0.684	0.02	0.08
Boredom susceptibility	92	63.96	9.86	93	65.71	9.26	0.216	0.01	- 0.002
Total score	92	16.63	3.59	93	16.77	3.52	0.787	0.07	- 0.01
Attentional impulsiveness	92	22.94	4.37	93	24.07	4.44	0.084	- 0.03	0.03
Motor impulsiveness	92	24.38	4.52	93	24.75	3.72	0.544	- 0.014	- 0.04
Non-planning impulsiveness	94	42.19	8.52	94	40.16	8.07	0.095	- 0.043	- 0.018
Neuroticism	94	50.99	8.94	94	56.03	8.97	<0.001**	0.081	0.052
Extraversion	94	53.59	9.33	94	56.38	9.31	0.042*	0.015	- 0.009
Openness	94	52.86	10.68	94	52.48	9.54	0.796	- 0.049	- 0.090
Agreeableness	94	50.32	9.43	94	52.43	8.08	0.101	- 0.069	- 0.006
Conscientiousness									
Age (years)		20.70	1.59		20.77	1.65	0.78		
Gender (n)									
Male	47			47					
Female	47			47					
Race/Ethnicity (n)							$\chi^2 = 0.79$		
Caucasian	69			72					
African American	1			1					
Asian	15			12					
Pacific Islander	2			1					
Other	7			8					
Education (years)		14.26	1.28		14.52	1.17	0.14		

Measures	low TAS (n = 94)			high TAS (n = 94)			t-Test	RGT Corr. r	
	n	Mean	S.D.	n	Mean	S.D.		Risky (no prior punishment)	Risky (prior punishment)
Total lifetime use									
Stimulants		23.94	66.18		21.82	62.8	0.82		
THC		675.06	1200.4		679.9	1455.7	0.98		
Cocaine		25.57	105		15.58	30.22	0.37		
MDMA		1.96	3.94		3.07	5.21	0.10		

SS: Sensation Seeking Scale Form-V, BIS: Barratt Impulsiveness Scale, NEO: NEO-FFI Five Factor Inventory;

* p < .05,

** p < .01

Table 2

Areas with significant group differences in a whole brain analysis for the interaction between level of risk and level of gain (risky-gains task) as a result of the LME (1024 μ l volume-thresholded cluster center of mass coordinates), as well as contrasts addressing the relative difference of BOLD signal in gains $\Delta+$ (+40 vs. +80) and losses $\Delta-$ (-40 vs. -80) in high vs. low TAS individuals.

Volume (μ l)	x	y	z	L/R	Area	BA	F – statistics F-crit = 6.77 F (1,186)/p=0.01	BOLD difference in gains $\Delta+$ and losses $\Delta-$ in high vs. low TAS $\Delta+$ high TAS > $\Delta+$ low TAS	$\Delta-$ high TAS < $\Delta-$ low TAS
8064	-18	-61	41	L	precuneus	7	15.32	0.202 > 0.063 **	0.029 < 0.153 **
3968	-48	-44	-3	L	middle temporal gyrus	37	13.76	0.165 > 0.046 **	0.028 < 0.089 *
3904	-37	-10	-6	L	insula	21	15.26	0.139 > 0.052 **	0.036 < 0.050
3776	-36	36	3	L	inferior frontal gyrus	46	9.80	0.105 > 0.005 **	0.029 < 0.089
2880	53	-47	-4	R	middle temporal gyrus	37	17.52	0.242 > 0.073 **	0.054 < 0.150 *
2432	-23	2	13	L	lentiform nucleus		9.52	0.256 > 0.030 **	0.060 < 0.160
2368	13	11	-5	R	nucleus accumbens		11.83	0.114 > 0.067 *	0.003 < 0.062 *
1856	26	0	60	R	superior frontal gyrus	6	10.84	0.248 > 0.101 **	0.008 < 0.166 **
1664	-9	0	-8	L	subcallosal gyrus	34	10.34	0.158 > 0.048 **	0.067 < 0.074
1344	22	-54	35	R	precuneus	31	10.37	0.308 > 0.112 **	0.046 < 0.194 **
1216	-47	-6	29	L	precentral gyrus	6	8.84	0.164 > 0.089	0.041 < 0.150 *
1152	9	47	37	R	superior frontal gyrus	8	12.67	0.088 > 0.011 **	0.018 < 0.054
1088	-5	37	50	L	superior frontal gyrus	8	10.93	0.230 > 0.070 **	0.013 < 0.115 *

* p < .05,

** p < .01

Table 3

Areas with significant group differences in a whole brain analysis (interaction between level of risk and level of gain in the risky-gains task) that show a correlation between the relative difference of BOLD signal $\Delta 80$ when winning (+80) or losing (-80) and changes in behavior following punishment ("change to safety behavior").

L/R	Area	BA	Corr. $r_s \Delta 80$ and change to safety behavior		
			low TAS (n = 94)	high TAS (n = 94)	all subjects (n = 188)
L	precuneus	7		-0.224*	-0.180*
L	middle temporal gyrus	37			
L	insula	21		-0.237*	-0.197**
L	inferior frontal gyrus	46			
R	middle temporal gyrus	37		-0.227*	
L	lentiform nucleus			-0.234*	-0.174*
R	nucleus accumbens				-0.164*
R	superior frontal gyrus	6		-0.301**	-0.151*
L	subcallosal gyrus	34			-0.189**
R	precuneus	31			
L	precentral gyrus	6			
R	superior frontal gyrus	8			
L	superior frontal gyrus	8			

* $p < .05$,

** $p < .01$