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**Taking Risks to Feel Excitement:**

**Detailed Personality Profile and Genetic Associations**

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**Abstract**

This study mapped the personality and genetics of risky excitement-seekers focusing on skydiving behavior. We compared 298 skydivers to 298 demographically matched controls across the NEO Personality Inventory-3 domains, facets and 240 items. The most significant item-level effects were aggregated into a poly-item score of skydiving-associated personality markers (SPM; Study 1), where higher scores describe individuals who enjoy risky situations but have no self-control issues. The SPM score was associated with greater physical activity, higher rate of traumatic injuries and better mental health in a sample of 3,558 adults (Study 2). From genetic perspective, we associated skydiving behavior with 19 candidate variants that have previously been linked to excitement-seeking (Study 1). Polymorphisms in the SERT gene were the strongest predictors of skydiving, but the FDR-adjusted *p*-values were non-significant. In Study 2, we predicted SPM and E5: Excitement-seeking from risk-taking polygenic scores (PGS), using publicly available summary data from genome-wide association studies. While E5: Excitement-seeking was most strongly predicted by general risk tolerance and risky behaviors' PGSs, SPM was most strongly associated with the adventurousness PGS. Phenotypic and PGS associations suggest that skydiving is a specific — perhaps more functional — form of excitement-seeking, which may nevertheless lead to physical injuries.

Keywords: five-factor model; excitement-seeking; polygenic scores; risk-taking; skydiving

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Individuals differ considerably in terms of how much they enjoy and pursue activities that are exciting, and how eager they are to try new intense experiences that may be dangerous. The constructs that have most often been used to describe these differences are excitement-seeking, which is a facet of Extraversion in the Five-Factor Model of personality (FFM; Costa & McCrae, 1992; Terracciano et al., 2011), sensation seeking (especially its subtype thrill- and adventure-seeking; Zuckerman, 1994), novelty-seeking (Cloninger et al., 1993), behavioral activation system sensitivity (Carver & White, 1994), and also parts of the multi-faceted construct impulsivity (Whiteside & Lynam, 2001). Common to all these constructs is the tendency or willingness to experience a thrill that life- or injury-threatening encounters usually evoke. The existing multitude of phenotypes of risk-taking due to a myriad of theoretical models and methodological approaches has not simplified studying their possible underpinnings. In the present study, we exclusively focus on risk-taking behavior, which is oriented towards feeling excitement through different activities and experiences, examining in depth its underlying personality characteristics and the possible contribution of different genetic polymorphisms.

**Risk-taking as a Personality Trait**

Willingness to take risks has shown to be highly reliable across time, indicative of a stable psychological trait (see Frey et al., 2017). The sensation seeking trait has probably been most thoroughly studied in the context of personality and risk-taking: it seems to be related with the proneness to highly stimulating activities such as adventure sports, but also to higher likelihood of consuming exotic meals, taking drugs, having more sex, being involved in illegal activities, and so forth (Aluja et al., 2003; Zuckerman, 1994). Individuals who take risks should, however, not be viewed as a homogenous group, as there seem to be domain-specific clusters in risk-taking that may have different sources of inter-individual differences (cf. Boldak & Guszkowska, 2013). For instance, according to Frey and colleagues (2017), recreational risk-taking is probably triggered by a desire for "thrill and adventure seeking," while risk-taking with adverse health effects (such as alcohol intake and smoking) occurs mainly because of problems with controlling inhibitory processes (Frey et al., 2017).

Cooper and colleagues (2000) have theorized that different personality traits are associated to different risk-taking domains or behaviors due to distinct emotion-related motives—coping and enhancement. Neuroticism primarily drives motivated risk-taking to regulate negative affect. For instance, Woodman and colleagues (2009) have stated that high risk sport environment may specifically help alexithymic persons (who are characterized by a subclinical difficulty describing and identifying emotions) to regulate their anxiety. Extraversion (or Surgency), on the other hand, is primarily associated with the strategic use of risky behaviors to enhance positive affective experiences (Cooper et al., 2000). Motives associated with affect regulation, however, do not explain the robust associations between low Conscientiousness and risky health behaviors (Bogg & Roberts, 2013).

Using only a limited set of broad personality traits such as Neuroticism and Extraversion, or relying solely on the sensation seeking model, may result in significant loss of valuable information. For instance, Castanier and colleagues (2010) classified individuals involved in high-risk sports into discrete personality types and concluded that configurations of low Conscientiousness combined with high Extraversion and/or high Neuroticism were associated with greater risk-taking (Castanier et al., 2010). The findings of the Basel-Berlin Risk Study revealed additional contributions of Openness to Experience (positive) and Agreeableness (negative) to risk preferences (Frey et al., 2017). But even this multi-method and psychometrically sophisticated study did not reveal which aspects of these broad personality traits precisely drive the associations with taking different kinds of risks. There is some evidence, though, that the sensation seeking trait is not only associated with broad personality domains but also with different lower-level facets, such as E5: Excitement-seeking (a facet of Extraversion) as well as O4: Actions and O1: Fantasy (facets of Openness to Experience; Aluja et al., 2003).

**Specific Personality Traits below Broad Dimensions.** A challenge for personality researchers is to identify a level of abstraction which, for their specific research question, represents the best compromise between inclusiveness and parsimony on the one hand (i.e., bandwidth), and informativeness and accuracy on the other (cf. Cooper et al., 2000). Personality has been shown to be linked with a wide range of social, mental, and physical health outcomes (Ozer & Benet-Martinez, 2006; Roberts, Kuncel et al., 2007) and in several studies, the narrower facets of the FFM dimensions have shown to be more closely associated with different behavioral outcomes and to account for more variance in behavioral criteria than the Big Five factors or domains alone (Paunonen & Ashton, 2001). Moreover, each facet carries, beside common information shared by other facets, specific information called nuances (McCrae, 2015). Mõttus and colleagues (2017) showed that even single items have their unique information which can contribute to the prediction of the life outcomes and sometimes the observed trait–outcome associations may be driven solely by specific nuances (Mõttus et al, 2017). For instance, Vainik and colleagues (2015) demonstrated that the N5: Impulsiveness–Body Mass Index association mostly depends on only two eating-related items, suggesting that the trait associated with Body Mass Index “may be narrower than the trait the N5: Impulsiveness scale is supposed to measure” (p. 622). In the similar vein, the E5: Excitement-seeking facet of Extraversion in the NEO PI-R/3 personality inventory (Costa & McCrae, 1992) consists of eight items which values are usually summed up to a total score. Although all items reflect the tendency to seek excitement in certain way, some items pertain to taking risks for the sake of feeling excitement (e.g., *craving for excitement* (#22) and *doing* *things just for "kick"* (#82)) while others capture a more laid-back way of obtaining stimulation (e.g., *enjoying loud music* (#202) and *enjoying attending games* (#232)). Thus, examining personality effects at only the facet level may not tell us enough about someone's specific risk-taking behaviors or tendencies. To overcome this problem, we will also examine the unique constellation of personality nuances in this study. That is, we will analyze personality data not only at the level of domains and facets but also at the level of items (i.e., nuances).

**Genetics of Risky Excitement-Seeking**

Behavioral genetic (mostly twin and adoption) studies have shown that risk-taking and excitement-seeking have a substantial biological basis with roughly 50% of its variance being heritable (Jang et al., 1998). According to Kandler and colleagues (2010) who examined the common variance in self- and informant reports in hundreds of twin pairs, there is substantial facet-specific variance of excitement-seeking over and above Extraversion and this component is mainly attributable to genetic differences. After systematically reviewing the literature, we identified a list of candidate genes and single nucleotide polymorphisms (SNPs) within these genes, which had been found linked to risk-taking, excitement-seeking and other related constructs in previous studies (see Table 1). As can be seen, most of the potential genes/variants are associated to the function (synthesis, transport, and degradation) of two neurotransmitters, dopamine and serotonin (e.g., Netter et al., 1996; Heck et al., 2009). High sensation seeking scores are hypothesized to have upregulated (increased release) dopaminergic systems, based on exposure to stressors, and increased release from dopaminergic systems usually correlate with decreased release from serotonergic and norepinephrine systems (Roberti, 2004). However, the initial findings concerning the most studied gene linked to sensation-seeking, the D4 dopamine receptor (DRD4) gene, have not been replicated in subsequent meta-analyses (Sanchez-Roige et al., 2018). A connection between different personality traits (such as novelty-seeking and harm avoidance) and monoaminergic neurotransmitter systems has received scrutiny since being suggested by Cloninger (1987) in his biosocial model of personality (more detailed information about the neurotransmitter systems associated with the selected candidate genes is outlined in Table S1 in supplemental materials).

Despite extensive research and some very promising initial progress in behavioral genetics, the beginning of the era of the genome-wide association study (GWAS) demonstrated that many and sometimes even the majority of previously established candidate genes are false signals produced by noise, which exceeded useful signals. For example, only two genetic loci were associated with self-reported risk-taking in a GWAS using 116,255 UK Biobank participants (Strawbridge et al., 2018). One of the most recent GWAS of risk tolerance and risky behaviors in a combined sample of over 1 million individuals by Karlsson Linnér and colleagues (2019) indicated that fifteen most commonly tested candidate genes in the prior literature on the genetics of risk tolerance were not particularly strongly associated with general risk tolerance or specific risky behaviors. Thus, most claims of associations between genetic variants involved in increased risk-taking are so far based on small-sample underpowered candidate gene association studies that assumed that the loci under investigation would have significantly larger effect sizes than GWA studies showed (Sanchez-Roige et al., 2018). As nicely articulated by Plomin (2018), the candidate gene approach expected to discover gold nuggets but "what GWA studies found was gold dust …. Each speck of gold was not worth much but scooping up handfuls of gold dust makes it possible to predict genetic propensities of individuals" (p. 214).

Although the candidate gene studies of personality (as well as specifically risky behaviors) have serious limitations (e.g., Munafò & Flint, 2011), especially when considering the likely polygenic nature underlying personality traits, a hypothesis-driven selection of promising polymorphisms is a meaningful and cost-effective approach, especially when studying unique or small populations (Jorgensen et al., 2009). One possible approach is relying on these previous studies, which have identified a number of SNPs associated with excitement and sensation seeking and examine these jointly. We do not expect that any of these SNPs listed in Table 1 are able to explain excitement- and sensation seeking behavior alone, but we believe that there may be value in examining whether these literature-proposed genes together will be able to explain a detectable proportion of the observed variance in risky excitement seeking behavior or not.

Another approach, which has become available more recently is constructing polygenic scores (PGS) from the 'weights' derived from previous GWA studies. Aggregating the effects of many SNPs in polygenic scores yields a genetic index that can capture substantial parts of the variation in complex behavioral traits. In polygenic scoring, researchers take results from a GWAS of a specific trait and apply them in a new sample, weighting each person's genetic variants by the effect size from the GWAS and summing across the variants. The resulting PGS is therefore a linear index summarizing an individual's overall genetic liability towards a phenotype (Wray et al., 2014). PGS can be constructed for any complex genetic phenotype for which appropriate GWAS results are available (Duncan et al., 2019). According to Karlsson Linnér et al. (2019), the risk-taking SNP heritabilities ($h^2_{\mathrm{SNP}}$) are between 4.6% for general risk tolerance and 9.8% for adventurousness. For the first principal component of the four risky behaviors (smoking, drinking, speeding, and number of sexual partners) the SNP heritability is reportedly higher, i.e., $h^2_{\mathrm{SNP}}$ = 15.6% (Karlsson Linnér et al., 2019). The present study aimed to benefit from both of these genetic approaches – specific candidate gene variants were analyzed using a relatively extreme group of excitement-seeking risk-takers (i.e., skydivers; Study 1) and PGS were calculated based on the association results of previous large-scale GWA studies of risk-taking and examined in a larger population-based cohort (in Study 2).

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Insert Table 1 about here

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**The Present Research**

One of the best strategies to study excitement- and sensation seeking is to examine extreme risk-taking groups such as skydivers (cf. Boldak & Guszkowska, 2013; Frey et al., 2017; Myrseth et al., 2012; Prochniak, 2011; Woodman et al., 2009). Skydiving (especially doing solo parachute jumps) represents taking calculated risks for the sake of thrills and excitement through an intense physical activity. The act of skydiving is usually well planned and most often it is preceded by a careful consideration of danger and apprehension of risks (possible injuries or even death; Westman et al., 2010). From this description, it is clear that skydiving is not an activity that happens as a consequence of poor impulse control but rather as a well-considered and carefully planned decision (cf. Myrseth, 2012). For this reason, we conceptualized solo skydiving as a concrete and objectively observable real-world risky behavior, conducted mostly for the sake of feeling excitement.

The first aim of present research is to find a set of personality characteristics, which are most strongly associated to excitement-seeking risky behavior, more specifically to skydiving. In Study 1, we will explore this by comparing two groups of individuals—skydivers and individuals who had not skydived but were demographically similar to them. As already said, failure to examine other personality-related factors may overestimate the role of impulsivity in risk-taking (Cooper et al., 2000). In other words, there may be considerably more complex associations between personality traits and risk-taking. Therefore, in Study 1 we report (and in Study 2 aim to validate in a large population-based sample) the results of a thorough analysis of the relations between excitement-oriented risk-taking behavior and the FFM traits at different levels of personality hierarchy, including domains, facets, and nuances. The findings of these analyses may have important health-related implications, because while excitement-seekers might not always be dealing with issues of low impulse control, their risk-taking preferences could also have real and potentially harmful consequences. However, as risk-taking and excitement-seeking can take several forms, it is obvious that not all excitement-seeking has adverse health consequences. As an example, although sensation seekers might be more active smokers, they may at the same time have lower blood pressure compared to low scorers of sensation seeking (Zuckerman, 1988). This might seem contra-intuitive, but sensation seeking has many behavioral correlates in addition to alcohol and substance usage (Roberti, 2004). Stimulating vocations, high risk sports and other types of sports involvement require a considerable level of physical activity; being regularly and moderately physically active has numerous favourable health benefits, even extending longevity (Blair & Morris, 2009). Thus, higher levels of excitement-seeking can instead be associated with fewer health issues. In this study we strive to find out if the personality traits that are associated to excitement-seeking-oriented risk-taking are also linked to a set of general health indicators (e.g., BMI, diagnosed diseases, blood pressure, mental health, and doing physical exercise) as well as to specific risky behaviors (e.g., substance use, extreme sports participation) and their potential consequences (e.g., probability of traumatic injuries).

Our second research question deals with the associations between the excitement-seeking risky behavior and genetic polymorphisms by combining two approaches – the candidate gene approach and the GWAS-based multi-polygenic score approach. In Study 1 we examined potential contributions of the candidate genes of excitement-seeking identified by previous genetic studies by comparing skydivers to a control group. In Study 2, we analyzed whether the set of skydiving-related personality characteristics found in Study 1 could be predicted from several risk-taking-related PGS in a large population-based cohort in order to further explain the genetic underpinnings of skydiving-related personality markers.

Our study goes beyond existing evidence on the personality correlates of sensation seeking in several important ways. The main novelty of this research lies in the technique that was used for identifying the most significant personality markers of excitement seekers. Namely, the most relevant personality markers of excitement-oriented risk-taking were identified in a unique sample of skydivers (Study 1) and validated in a large population-based sample using relevant behavioral indicators as well as risk-taking-related PGSs (Study 2). Secondly, this study examined personality correlates of excitement-seeking risky behavior at three different levels of analysis – domains, facets, and items. And thirdly, the present study re-examined the excitement-seeking candidate gene approach by predicting skydiving behavior from previously reported candidate gene polymorphisms.

## Study 1

Study 1 explored the relative contribution of different personality characteristics and literature-proposed genetic variants to excitement-seeking risky behavior—more specifically, skydiving. Skydiving is related to serious health risks, but at the same time, it is a socially acceptable and non-pathological way to fulfill the need to experience excitement and thrill (Myrseth et al., 2012). Skydivers have been shown to obtain higher scores on measures of sensation seeking than mountain climbers or car racers (Jack & Ronan, 1998). Comparing skydivers to demographically matched controls enables to pinpoint the most significant personality characteristics or markers that differentiate skydivers from people who are not willing to take such risks. In this study we examined the associations of these so-called skydiving personality markers (combined into an item risk score) to a set of skydiving-related as well as more general risk and health indicators in comparison with the NEO PI-3 E5: Excitement-seeking facet, which is a frequently used FFM-based scale for measuring risk proneness. Among the more traditional risk indicators (such as substance use) we also examine the probability of traumatic injuries – physical traumas that have been acquired in relation to the act of skydiving as well as the overall tendency of having experienced traumatic injuries (such as bone fractures). Skydiving itself might not be the most dangerous extreme sports – according to the largest epidemiological studies of skydiving-related injuries, the incidence of non-fatal injury events is 48-49 per 100,000 jumps (Fer et al., 2020; Westman & Björnstig, 2007). However, we hypothesize that due to skydivers' heightened excitement-seeking-oriented risk-taking tendencies, they might be more prone to engage in a variety of daring activities (linked to, for example, sports or traffic) that could result in higher probability of having experienced traumatic injuries, compared to the normal population.

In the second part of Study 1, we compared the group of skydivers to their matched controls across the candidate gene SNPs of excitement-seeking and risk-taking identified by previous genetic studies (see Table 1). Our approach is similar to genetic association case–control studies, where individuals with and without a given disease trait are compared against each other, in order to determine whether a statistical association exists between the disease trait and the genetic marker (Clarke et al., 2011). The advantages of selecting individuals from the tail(s) of the quantitative distribution of a phenotype in genetic association studies include increasing the probability of the presence of risk alleles in the sample and decreasing the cost of genotyping (Li et al., 2019).

In sum, the aims of Study 1 were to find out (a) which set of personality characteristics would be most strongly associated to excitement-seeking risky behavior (i.e., skydiving), and (b) if and to what extent the candidate genes of excitement-seeking, as identified by previous genetic studies, could contribute to explaining skydiving behavior.

**Method**

**Ethics Statement.** Ethical approvals for this study were obtained from the Research Ethics Committee of the University of Tartu (protocol numbers 205T-12 (2011) and 237/M-10 (2014)). The study was not pre-registered.

**Subjects.** The total sample of Study 1 consisted of 298 Estonian skydivers and of 298 demographically matched control individuals.

***Skydivers.*** The group of skydivers consisted of 194 males (65%) and 104 females (35%). Their age ranged from 16 to 69, with mean age of 32.4 (*SD* = 7.9) years. The majority of this group (60%) had university education, followed by general secondary (21%), vocational secondary (18%), and compulsory education (1%) (see Table 2). The mean number of jumps per skydiver was 164 (*SD* = 320), ranging from 1 to 1,850 jumps (*median* = 12). Altogether 45 individuals (15%) in the skydivers' group had performed only one parachute jump, whereas half of the group (194 individuals) had performed 2 to 59 jumps. Fourteen (5%) skydivers had performed over 1,000 parachute jumps. Altogether 23 individuals in the sample were professional skydivers whose mean count of parachute jumps was considerably higher (*mean* = 361, *SD* = 499, *median* = 20) compared to the participants for whom skydiving was a leisure-time activity (*mean* = 146, *SD* = 294, *median* = 12). Ten individuals (3%) had completed a BASE jump (i.e., parachuting from buildings, antennas, spans, or cliffs, for instance). Sixty-one per cent (179 individuals) had skydived in the past 12 months.

Data were collected from 2011 to 2014. After signing an informed consent form and providing the saliva sample for DNA extraction, the majority of skydivers (*n* = 290, 97%) filled in the questionnaires online, using the web-based research portal of the Institute of Psychology, University of Tartu. The remaining eight skydivers filled in paper questionnaires. Initial sample size was 302, but four skydivers were excluded due to missing personality or demographic data.

***Controls Matched to Skydivers.*** Controls for Study 1 were drawn from the population-based Estonian Biobank of the Estonian Genome Center at the University of Tartu (EGCUT; for details see Leitsalu et al., 2014; and Study 2 of the current paper) for whom both comparable genome-wide microarray as well as personality data were available. The control group was otherwise randomly chosen with the only prerequisite of demographic similarity to the sample of Estonian skydivers. More specifically, 298 Biobank participants from the larger sample who were the closest match to each of the skydiver in terms of age, gender, and education level were chosen automatically (see Statistical Analysis). The age of these individuals ranged from 18 to 69 (*mean* = 32.5, *SD* = 7.9), and there were 195 men (65%) in this control group. Altogether 59% (*n* = 177) of this subsample had tertiary university education, about 19% (*n* = 57) had vocational secondary education, 21 % (*n* = 61) of the controls had secondary education, and 1% (*n* = 3) had basic compulsory education.

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Insert Table 2 about here

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**Materials.**

***FFM Personality Traits.*** Personality traits and facets were measured using the NEO Personality Inventory-3 (NEO PI-3; McCrae, Costa, & Martin, 2005). The NEO PI-3 is a slightly modified version of the NEO PI-R questionnaire (Costa & McCrae, 1992) which was adapted into Estonian by Kallasmaa and colleagues (2000). The NEO PI-3 measures five broad factors—Neuroticism, Extraversion, Openness to Experience, Agreeableness, and Conscientiousness—and their altogether 30 facets. For instance, Excitement-seeking (E5) is a facet of Extraversion, and (similarly to other facets) it is measured by 8 items, which are answered on a 5-point Likert scale, ranging from 0 *(strongly disagree)* to 4 *(strongly agree).* McDonald’s omegas (Zinbarg et al., 2006) of the facet scales ranged in this sample (*N* = 598) from .67 (for O6: Values) to .89 (E4: Activity and E6: Positive Emotions); with the average omega of .82. The McDonald's omega of E5: Excitement-seeking was .78. As the NEO PI-3 (McCrae et al, 2005) is copyright protected, it is not open to the public.

***Information on Health and Risk Indicators.*** Skydivers filled in additional self-report questionnaires about their skydiving and other extreme sports activities, general health status and habits, and basic demographic characteristics. Among other questions, skydivers were asked (*yes* or *no*): *"Have you ever smoked?"* (55% ($n$ = 163) answered *yes*), *"Have you ever used narcotic or psychotropic drugs?"* (53% ($n$ = 158) answered *yes*[1]), *"Have you ever had any bone fractures or other traumatic injuries?"* (57% ($n$ = 170) answered *yes*), *"Do you do any physical exercise?"* (81% ($n$ = 240) answered *yes*), *"Do you practice any other extreme sports besides skydiving?"* (56% ($n$ = 176) answered *yes*), and "*Have you experienced any skydiving-related injuries?"* (26% ($n$ = 77) answered *yes*). Based on self-reported weight and height, body mass index (BMI) was calculated as weight/height$^2$ (kg/m$^2$). Average BMI of skydivers was 24.0 ($SD$ = 3.3).

**Genotyping.** In case of skydivers, genomic DNA was extracted from saliva (using the PSP *SalivaGene DNA Kit*). For individuals in the control group, genomic DNA was extracted by standard procedures from peripheral blood samples, which were provided when they first joined the biobank of the EGCUT. The captured DNA was genotyped using the Illumina Infinium II (Illumina Inc., San Diego, CA, USA) technology, according to the manufacturer's protocol. Genotyping was performed on multiple Illumina platforms. For the control group, the Illumina CNV370-Duo BeadChip platforms were used for 12 individuals; Human OmniExpress BeadChips for 101 individuals; HumanCoreExome-12 v1.0 BeadChips for 185 individuals. For the whole skydivers' group, genotyping was performed on the HumanCoreExome-12 v1.0 BeadChip platform. Missing genotypes were imputed using the 1000 Genomes phase 3 (The 1000 Genomes Project Consortium, 2015) reference panel.

Imputation was performed with IMPUTE v2 (Howie et al., 2009). SNPs with imputation quality < 0.8, call rate < 95%, and minor allele frequency <1% were excluded from further analysis. Individuals were excluded if they had a call rate < 99%, and we also excluded related individuals (PIHAT ≥ 0.2).

***RFLP-Based Genotyping.*** Restriction fragment length polymorphism analysis of PCR-amplified fragments (PCR-RFLP) was performed in case of the DRD4, SERTPR, STin2, and the AR (GGN and CAG) polymorphisms. The alleles at the respective loci were amplified from genomic DNA using polymerase chain reaction (PCR). The PCRs were performed using ThermoScientific Arktik Thermal Cycler. PCR products were then run on an ABI 3100 Genetic Analyzer (Applied Biosystems), and scored using the software GeneMapper 4.1 (Applied Biosystems). All genotypes were manually checked on chromatograms to detect inconsistencies, and, where needed, amplified and scored the second time. Rox500 (PE Applied Biosystems) was used as an internal size marker standard[2]. The specific PCR protocols (PCR cycles and reaction mixes) as well as primers can be found in supplemental materials (Table S2), which can be accessed here.

Repeat numbers were dichotomized into short *versus* long alleles, based on previous studies (e.g., Ebstein et al., 1998), or using their respective mean as cut-off point (in case of the AR gene polymorphisms). In case of the DRD4 VNTR polymorphism, allele containing 5 or fewer repeat elements was classified as short allele, and an allele with 6 or more repeats as a long allele (as indicated in the meta-analyses by Kluger et al., 2002). For the STin2 VNTR variant, alleles containing 9 or 10 repeats were classified as short, and alleles containing 12 repeat elements as long (similarly to Fan & Sklar, 2005). In case of the SERTPR polymorphism, the lower expressing allele with 14 repeats was classified as short, and the higher expressing allele containing 16 repeats was classified as long (see Fan & Sklar, 2005). For the AR gene CAG variant, alleles containing 21 or fewer repeat elements were grouped as short alleles, and alleles with 22 or more repeats were grouped as long alleles (as in Simmons & Roney, 2011). And for the GGN variant, 23 and less repeats were classified as a short allele, whereas alleles containing 24 or more repeat elements were classified as long alleles (as in the meta-analysis by Jiang et al., 2016). As the AR gene is located on the X chromosome, men have only two genotype configurations (’s’ or ’l’), whereas women have three (’ss’, ’sl’, or ’ll’). The frequencies of short and long repeat length alleles for DRD4, SERTPR, STin2, and the AR (GGN and CAG) polymorphisms across skydivers and controls are presented in Supplementary Table S3.

**Statistical Analyses**

Skydivers were matched to controls using Microsoft R Open 3.5.1 (R Core Team, 2013) with package *MatchIt* (Ho, Imai, King, & Stuart, 2011), using the method of nearest neighbor matching, which selects the closest eligible control unit to be paired with each treated unit (i.e., skydiver). Matching of samples was conducted, using age, gender, and education level of skydivers as covariates. The associations between skydiving and 240 NEO PI-3 items were analyzed using the regularization technique of Elastic Net (Tibshirani, 2011; package *glmnet* in *R*; Friedman et al., 2018), which produces a sparse regression model with good prediction accuracy (by decreasing the variance of parameter estimates and decreasing the size of the coefficients; Zou & Hastie, 2005). The binary dependent variable was being a skydiver (1) versus a member of the control group (0). The elastic net mixing parameter alpha was set to 0.99 (in order to get the most parsimonious model possible within the Elastic Net), and the optimal regularization parameter lambda (λ) was obtained using 10-fold cross-validation, using the *cv.glmnet* function. We used tuning parameter ‘lambda.1se’ (in this specific model, $s = 0.046$), which gives the most regularized model such that cross-validated error is within one standard error of the minimum. Associations between 19 literature-proposed candidate polymorphisms and skydiving were analyzed using binary logistic regression models (package *rms* and function *lrm* in R software; Harrell Jr, 2020). The binary dependent variable was again being a skydiver (1) versus a member of the control group (0). *T*-tests and correlation analyses were conducted using SPSS statistical software version 23.0 (IBM, New York, USA).

**Results**

**Personality Profile of Skydivers.** Our first aim was to find out whether the skydivers' personality profile was systematically different from that of individuals who had unlikely skydived, and if yes, how? Figure 1 demonstrates the *T*-scores (the population mean 50 with the standard deviation 10) for the skydivers (blue triangles) and the controls (black circles) for the five domain scores and 30 subscales. As expected, all mean values for the control group were very close to the normative value of the whole population. On 17 out of 30 NEO PI-3 facet scales the skydivers' mean scores were significantly different from the control group (marked by asterisks). The independent samples' *t*-test revealed that skydivers also differed from the control group on FFM domains. They scored significantly higher on Openness to Experience ($t$ = 8.01, Cohen's $d$ = .66) and Extraversion ($t$ = 5.71, Cohen's $d$ = .47), and lower on Neuroticism ($t$ = -6.70, Cohen's $d$ = .55) and Agreeableness ($t$ = -3.23, Cohen's $d$ = .12) ($p$s < 001; see Figure 1). There were no significant differences ($p$ < .05) between skydivers and controls for the broad dimension of Conscientiousness.

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Insert Figure 1 about here

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At the facet level, skydivers were more open to actions (O4, $t$ = 9.23, Cohen's $d$ = .73) and values (O6, $t$ = 8.08, Cohen's $d$ = .66), and had higher excitement-seeking (E5, $t$ = 7.58, Cohen's $d$ = .62) as well as activity scores (E4, $t$ = 6.96, Cohen's $d$ = .57) than the control group. Skydivers were also less anxious (N1, $t$ = -7.04, Cohen's $d$ = .58) and vulnerable (N6, $t$

= -6.86, Cohen's *d* = .56) than demographically matched controls (all *p*s < 001). There were no significant ($p < .05$) differences in N5: Impulsiveness, but skydivers had lower Deliberation scores (C6, $t = -4.35$, $p < 001$, Cohen's $d = .36$) than the control group, which also refers to hastiness, impulsivity, and impatience (for all facets, results from *t*-tests are provided in supplemental material, Table S4.1). Thus, the skydivers had a rather distinctive personality profile, which distinguished from the control group in each the FFM personality dimensions.

**Constructing the Skydiving Personality Markers Score.** Next, we aimed to discover the best personality markers for predicting skydiving behavior. To that aim, a binary logistic regression model was run, where belonging to the sample of skydivers (*versus* to control group) was predicted by 240 NEO PI-3 items (please note that for all items, results from *t*-tests comparing skydivers and controls are provided in supplemental material, Table S4.2). As this model contained a large number of inter-correlated predictors (i.e., mostly items within the same facet), we used the regularization (shrinkage and selection) technique of Elastic Net (Tibshirani, 2011). The technique of regularized regression has been often used in other fields, such as genetics, but also in connection with using personality questionnaire items as predictors of some outcome in several previous studies (e.g., Mõttus & Rozgonjuk, 2019; Seeboth & Mõttus, 2018). Seeboth and Mõttus (2018) found that item-models showed greater prediction strength (representing personality-outcome associations) than models built from the FFM domains. In this study, the regularized model selected 18 items out of the 240 (and 'zeroed' the coefficients of all other items) that were most strongly connected to skydiving: four items from Neuroticism, four items from Extraversion, six items from Openness, and two items from both Agreeableness and Conscientiousness. The items that most strongly (betas $|\gtrsim 0.1|$) associated with being a skydiver were the following: *enjoying risky situations* (#172[3]; E5: Excitement-seeking; beta = .42), *being unable to resist cravings* (#51; N5: Impulsiveness;

beta = -.39), *sometimes doing this just for "kick"* (#82; E5: Excitement-seeking; beta = .22), *letting imagination fly* (#33; O1: Fantasy; beta = .21); *feeling helpless and needing a lot of help* (#26; N6: Vulnerability; beta = -.14); *being liberal in moral principles* (#238; O6: Values; beta = .08); *planning before travel* (#210; C6: Deliberation; beta = -.06); and *thinking that politicians must pay more attention to human needs* (#29; A6: Tender-mindedness; beta = -.06). The regression weights of the other 10 items were smaller and can be found in Table S5 in supplemental materials. The eight items with the largest weights (as listed above) were subsequently combined into an aggregate item risk score – the Skydiving Personality Markers or the SPM score – while taking into account the regression weights of each item. In other words, for each individual, the eight NEO PI-3 item scores were multiplied by their respective beta weights (from the elastic net regression) and summed. For skydivers, the constructed SPM score ranged from -0.89 to 3.59 ($M$ = 1.9, $SD$ = 0.8), and for controls, from -1.52 to 3.37 ($M$ = 0.7, $SD$ = 0.8)[4].

**Associations of SPM and E5: Excitement-Seeking with Health and Risk Indicators.** As shown above, the eight-item SPM score included two items from E5: Excitement-seeking facet. Although the SPM and E5: Excitement-seeking scores were significantly correlated in the sample of skydivers ($r$ = .46, $p$ < .001), both scores/scales nevertheless had notable unique variance. In order to compare the effectiveness of the SPM and E5: Excitement-seeking in predicting health- and risk-related variables or their proxies, we conducted a series of regression analyses using the sample of skydivers ($N$ = 298). In all the models, several general as well as specifically skydiving-related health or risk variables were treated as the dependent or outcome variables, which were predicted by age and gender (in a baseline model) and SPM (Models 1) or the E5: Excitement-seeking (Models 2). In case of the continuous outcome variables (BMI and total count of parachute jumps), linear regression models were run, and for binary outcome variables (having smoked, having used drugs, having experienced traumatic injuries in general, having experienced skydiving-related injuries, engaging in other extreme sports besides skydiving, and doing physical exercise), logistic regression models were conducted. Results of these models are shown in Table 3. We found that the SPM was at least as effective as the E5: Excitement-seeking in predicting risk-related indicators within the skydivers' sample: both scales/scores predicted statistically significantly ($p < .05$) the probability of having used drugs and having smoked and participating in extreme sports besides skydiving (when age and gender of individuals were taken into account). However, the SPM score, but not the E5: Excitement-seeking facet, was also associated to the overall count of individuals' parachute jumps and the probability of having experienced skydiving-related injuries (see Table 3). Neither the SPM nor the E5: Excitement-seeking were significantly associated to skydivers' BMI, overall traumatic injuries, and doing physical exercise.

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Insert Table 3 about here

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**Genetic Polymorphisms Associated with Skydiving.** Next, we analyzed the differences between skydivers and controls in terms of different genetic polymorphisms that have been previously related to sensation seeking and related constructs (see Table 1 as well as Table S1 in supplemental materials). Information about the frequencies of alleles and genotypes of the literature-proposed genetic variants across skydivers and controls can be found in Table S3 in supplemental materials. Genotype frequencies of control group participants were for each of the genetic polymorphisms in Hardy–Weinberg equilibrium (HWE) ($p > .05$). In order to model the association between excitement-oriented risk-taking behavior (i.e., engaging in skydiving) and genetic polymorphisms, we conducted a binary logistic regression model using R (function *glm*, family *binomial*, link *logit*). In these models we estimated the probability of belonging to the group of skydivers, using 19 genetic variants and socio-demographic variables (age and gender) as predictors. The dependent variable was the binary indicator of belonging to the skydivers' sample *versus* to the control group, and it was predicted by 19 genetic polymorphisms while controlling for participants' age and gender. A baseline model with only age and gender as predictors had Nagelkerke $R^2$ of .003. After adding 19 genetic variants to the model, the Nagelkerke $R^2$ increased to .095 (whereas Cox & Snell $R^2$ was .071). Thus, with caution this result could be interpreted as 19 genetic variants explaining about 7% to 9% of being a skydiver (versus not), classifying correctly about 63.6% of participants (see Table 4)[5]. For comparison – the SPM score (which was designed with the aim of differentiating between skydivers and controls) explained 48% of variance in the dummy-coded skydiving status, classifying correctly about 77% individuals. There were altogether three genetic polymorphisms with *p*s < .05: SERTPR VNTR (in SERT gene; $z$ = -2.48, OR = 0.67, 95% CI [0.48; 0.92]), rs167771 (in DRD3 gene; $z$ = -2.31, OR = 0.62, 95% CI [0.41; 0.93]), and rs841 (in GCH1 gene; $z$ = -2.11, OR = 0.67, 95% CI [0.46; 0.97]). In addition, the SNP rs25531 (in SERT gene) also showed a statistical trend ($z$ = -1.91, $p$ = 0.056, OR = 0.58, 95% CI [0.33; 1.01]). However, when skydiving was predicted by one genetic variant at a time (i.e., separate logistic regression models were run in case of each of the 19 candidate gene polymorphisms), the SNP rs25531 explained the largest amount of variance in being a skydiver (change in Nagelkerke $R^2$ = .012), followed by the SERTPR vntr polymorphism (change in Nagelkerke $R^2$ = .009, see the last column in Table 4). Please note that none of these effects would not remain significant using a false discovery rate of 0.05 when using the Benjamini-Hochberg procedure for adjusting *p*-values.

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Insert Table 4 about here

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**Discussion of Study 1**

Comparing skydivers to demographically matched controls showed that self-reported personality traits have strong associations with skydiving, and that the E5: Excitement-seeking facet is only one part of the explanation (cf. Prochniak, 2011). Using regularized regression analysis, we constructed a short item risk score of skydiving-related personality markers (SPM), which included items not only from E5: Excitement-seeking but from all FFM domains and several facets such as N5: Impulsiveness, N6: Vulnerability, O1: Fantasy; O6: Values; A6: Tender-mindedness, and C6: Deliberation. The 8-item SPM score and the E5: Excitement-seeking facet were rather similarly associated to different health- and risk-related outcomes in the skydivers' sample, but the E5: Excitement-seeking was more strongly than the SPM score associated to having smoked and used drugs, whereas the SPM was more effective than the E5: Excitement-seeking facet in explaining total count of parachute jumps and the probability of skydiving-related injuries. Genetic polymorphisms (when analyzed jointly) also enabled to predict the probability of being a skydiver to some degree. However, as our exploratory analysis using simulated SNPs indicated, the overall amount of variance explained by candidate genes (which was altogether approximately 10%) could be an overestimation. Compared to the genetic contribution, a small set of answers to a personality questionnaire (such as in form of the SPM score) can tell us much more about whether a person would jump out of an airplane with a parachute for the sake of excitement from freefall. However, the SPM was designed to differentiate between skydivers and controls – the high proportion of explained variance in a logistic regression model using the same groups was expected. Whether this particular set of personality characteristics or nuances is indeed associated and generalizable to excitement-oriented risk-taking (and not just the very specific and rather extreme act of skydiving) has to be tested, using other (preferably large population-based) samples.

## Study 2

Findings from Study 1 demonstrated that using a relatively brief set of personality questionnaire items (stemming from across all the Five Factor traits) is an efficient way to differentiate between individuals who have taken the risk of a parachute jump and those who have not. The first aim of Study 2 was to examine how well the specially tailored item risk score of skydiving personality markers (SPM) that was constructed in Study 1 would work in describing real-life health consequences in a population-based sample of the Estonian Biobank. The SPM score was in the present study analyzed in the context of several health- and behavior-related indicators. Previous studies (e.g., the literature review by Roberti, 2004) have listed substance use, extreme sports participation, and risky sexual behavior as among the most relevant areas of sensation seeking. In addition to examining specific risk indicators or their proxies (e.g., smoking, using drugs, onset of alcohol use, the probability of STDs) we also analyzed indicators of general health (such as diagnosed diseases, objectively measured blood pressure and BMI, doing physical exercise, and self-assessed mental health status), because general physical activeness of excitement-seekers could have a positive impact on their general health (Blair & Morris, 2009). As a potential consequence of an excitement-seeking lifestyle we examine the probability of traumatic injuries. Although acquired traumatic injuries may have numerous causes, which are not often under the control of the individual, heightened excitement-seeking can be associated to engaging in a variety of daring physical activities – linked to sports (Sharma et al, 2015) or traffic (Turner & McClure, 2004), for instance – that could result in higher probability of having experienced traumatic injuries. This is by no means an exhaustive list of relevant variables, but it allows insight into the possible correlates and consequences of excitement-seeking-oriented risk-taking. The health- and behavior-related associations of the SPM score were – similarly to Study 1 –

compared with those of the NEO PI-3 E5: Excitement-seeking facet, in order to examine, whether the SPM is comparable with other existing measures in describing or explaining risky behaviors and specific health conditions. In short—in the first part of Study 2 we strived to find out if the SPM is useful in detecting individuals from normal population who tend to take more risks for excitement and thus have greater probability of getting into accidents.

The second part of Study 2 focused on genetic associations of excitement-seeking-related risk-taking (i.e., the SPM and E5: Excitement-seeking scores) using polygenic scores. In Study 1 we found a few polymorphisms that predicted skydiving behavior at the significance level of $p < .05$, but these associations were relatively weak and no longer significant when corrected for multiple comparisons. Moreover, it would be naïve to think that only a handful of core genetic variants contribute to the heritability of such a complex personality phenotype (Boyle et al., 2017). As indicated by the GWAS approach, the heritability of complex traits is likely spread across the whole genome, and therefore in Study 2, we examined the contribution of different risk-taking-related PGSs that have been constructed based on association results from previous large-scale risk-taking GWA studies (meta-analyzed by Karlsson Linnér et al., 2019). These resulting PGSs summarized individuals' genetic liability towards general risk tolerance and risk-related behaviors. In short, we aimed to examine whether the risk-taking PGS explain any variance in the SPM and E5: Excitement-seeking scores.

**Method**

**Ethics Statement.** Ethical approval for this study was obtained from the Research Ethics Committee of the University of Tartu (protocol number 236/M-29 (2014)). The study was not pre-registered.

**Sample.** For Study 2, the sample was again drawn from the population-based Estonian Biobank of the EGCUT. We used data of altogether 3,558 individuals (60% women, *n* =

2,124). This sample has been used in several published papers (e.g., Allik et al., 2016; Allik et al., 2018; Mõttus et al., 2017; Realo et al., 2017; Realo et al., 2018). The mean age of sample was 46.8 years (*SD* = 17.0, ranging from 18 to 91). Altogether 40% of the sample had tertiary university education, about 28% had vocational secondary education, 24% of the participants had secondary education, and 8% had basic compulsory education. Each participant signed an informed consent form (available at www.biobank.ee) and the physicians performed a standardized health examination of the participants. Participants also completed a computer-assisted personal interview (CAPI; the list of interview questions can be accessed here) on health-related topics and clinical diagnoses described in the WHO International Statistical Classification of Diseases and Related Health Problems, 10th Revision (ICD-10; Leitsalu et al., 2014).

**Materials.**

***Personality Traits.*** Personality traits and facets were measured using the Estonian version of the NEO Personality Inventory-3 (NEO PI-3; McCrae et al., 2005). The NEO PI-3 measures five broad factors—Neuroticism, Extraversion, Openness to Experience, Agreeableness, and Conscientiousness—and their altogether 30 facets, each of which is measured by eight items. In Study 2, we analyze the item risk score SPM, which was constructed from eight NEO PI-3 items belonging to different domains and facets (see Study 1), and the E5: Excitement-seeking facet (McDonald's omega = .79) from the NEO PI-3 Extraversion domain. As the NEO PI-3 is copyright protected, it is not open for the public.

***Health Status Indicators.*** All measures of physical and mental health status were retrieved from the EGCUT, which had gathered their data from the information provided by the participant, using the CAPI. Biometrical parameters (blood pressure, height, and weight) were measured by the EGCUT recruiters (Leitsalu et al., 2014).

*Blood Pressure.* Systolic and diastolic blood pressure (BP) was measured in sitting position at the end of the 1-2-hour long CAPI interview. Systolic BP ranged from 80 to 230 ($M$ = 126.00, $SD$ = 17.61), and the values of diastolic BP ranged from 50 to 135 ($M$ = 77.94, $SD$ = 10.75). Systolic and diastolic BP were strongly correlated ($r = .71$, $p < .001$). In order to avoid problems due to collinearity, only systolic blood was entered into the regression models. According to Palaniappan and co-authors (2002) who compared the usefulness of different blood pressure measures in predicting cardiovascular death (i.e., death due to coronary artery disease or stroke), systolic BP is the best single predictor of cardiovascular risk in untreated individuals.

*BMI.* Body mass index was calculated on basis of objectively measured weight and height during CAPI as weight/height$^2$ (kg/m$^2$). The values of BMI ranged from 15.62 to 54.08 ($M$ = 25.98, $SD$ = 4.87).

*Diseases Diagnosed.* During the CAPI, participants were asked, which kind of diseases they have been diagnosed with using the ICD-10 classification system. Three variables related to these diagnoses were used in present study: the total number of diseases for each individual, and the presence of diagnoses from the following two ICD categories: injuries and sexually transmitted diseases.

First, the mean number of diseases diagnosed *per* individual was 8.41 ($SD$ = 6.18), ranging from 0 to 61 diagnoses. Second, altogether about 12% of individuals ($n$ = 384) reported having experienced one or several injuries or poisoning incidents (from ICD-10 diagnose categories S00-T98: injury, poisoning and certain other consequences of external causes). And third, six percent of participants ($n$ = 203) reported having been diagnosed with one or several sexually transmitted diseases (STDs; from ICD-10 diagnose categories A50-A64: infections with a predominantly sexual mode of transmission).

*Mental health: Anxiety/depression.* The overall mental health status of participants was measured using a single question from the Estonian version of the EuroQoL Quality of Life Scale (Rabin & De Charro, 2001). This disease non-specific instrument consists of five different health dimensions (e.g., self-care and everyday activities), but in this study, only the dimension of anxiety/depression was analyzed. Participants were asked to indicate on a 3-point-scale which of the following three statements that were presented to them characterized their health status the best (1 – *"I do not feel anxious or depressed"*, 2 – *"I experience moderate anxiety or depression"*, and 3 – *"I feel very anxious or depressed"*). As only 31 individuals reported being very anxious/depressed, categories 2 and 3 were combined together, resulting in a binary variable. Altogether 35% of individuals in this sample ($n$ = 1,160) reported feeling anxious or depressed to a moderate or large degree.

***First Alcohol Consumption.*** During the CAPI, participants were asked: "How old were you when you first drank half a liter of beer, 100 ml of wine, 40 ml of liqueur at 20% vol or 40 ml of any type of fortified alcohol?" Mean age was 16.66 years ($SD$ = 3.22), ranging from 5 to 52 years of age.

***Using Drugs.*** Drug use was measured by the following question: *"In addition to alcohol and tobacco, have you used any other drugs?"* (answered *yes* or *no*). Altogether 7% of individuals ($n$ = 174) reported having used drugs.

***Smoking.*** Smoking was measured using the following two questions: *"Have you ever been smoking (more than just one time experience)"* (answered *yes* or *no*), and *"How old were you when you started to smoke regularly?"*. Altogether 37% of the sample had smoked ($n$ = 1,331), and the mean age of starting to smoke regularly was 19.18 ($SD$ = 5.01).

***Doing Physical Exercise.*** Participants were asked: *"Have you done or are doing physical exercise?"* (answered *yes* or *no*). Altogether 71% of individuals ($n$ = 1,767) reported doing some physical exercise.

**PGSs of General Risk Tolerance and Risky Behaviors.** Genotyping was performed on all participants using Illumina array Infinum Global Screening Array-24, imputed to Estonian reference based on imputational panel (Mitt et al., 2017). We implemented the same quality control procedure as outlined in Arumäe et al. (2021) supplement (https://osf.io/cmzv4/). Briefly, we filtered out poorly covered SNPs and participants, the major histocompatibility complex, and SNPs having minor allele frequency below 5%. We also filtered the GWASs to have minor allele frequency over 0.01. We used PRSice 2.31e[15] default clumping parameters ($R^2$ = .1, distance = 1000kb) for polygenic scores. For further details, see Arumäe et al. (2021). The 10 principal components were used as covariates in regression analyses of PGSs to control for any population stratification differences (Hamer & Sirota, 2000). The seven PGSs used in this study (general risk tolerance, ever smoker, drinks per week, number of sexual partners, automobile speeding propensity, the first principal component of four risky behaviors, and adventurousness) were trained on the GWAS results from Social Science Genetic Association Consortium (Karlsson Linnér et al., 2019). As per Lee et al. (2018), we report results that were obtained using no *p* criterion cut-off (*p* = 1), but did use PRSice default clumping criteria ($r^2$ threshold for clumping = .10; clumping distance = 1000kb). We decided *a priori* to use PGSs with no cut-off, as previous evidence suggests that this approach maximizes predictive ability of well-powered PGSs of complex traits, such as education (Lee et al, 2018). Having as many SNPs as possible also maximizes the pleiotropic nature of PGS–SPM associations. This matches with our goal to demonstrate any potential overlap between PGSs and SPM. However, results concerning PGSs using different p-value thresholds (*p* = .0001, *p* = .001, *p* = .01, *p* = .05, *p* = .1, and *p* = .5) can be seen in Supplemental Material, Table S8. After matching with available variants in the data, and clumping, the number of variants in PGS varied from 118,491 (‘ever smoker’) to 119,156 (‘drinks per week). The polygenic score of adventurousness included only 126 variants after clumping, as the GWAS of adventurousness was based on the 23andMe research cohort (see Karlsson Linnér et al., 2019). The personal genetics company 23andMe Inc. publicly provides altogether 10,000 most strongly related SNPs.

All seven PGSs were calculated on basis of the meta-analyzed association results reported by Karlsson Linnér et al. (2019). In these GWA studies, the seven phenotypes were coded such that higher phenotype values were associated with higher risk tolerance or risk taking. The general risk tolerance GWA studies were based on the questions: "*Would you describe yourself as someone who takes risks? Yes / No.*" (in the UK Biobank cohort) and *"In general, people often face risks when making financial, career, or other life decisions. Overall, do you feel comfortable or uncomfortable taking risks?"* (in the 23andMe cohort). In the ever-smoker GWAS, the smoking status was coded as *1* if a respondent reported that they were a current or previous smoker and *0* if they reported never smoking or only smoking once or twice. The sexual partners GWAS was based on the question: *"About how many sexual partners have you had in your lifetime?"*. The automobile speeding propensity GWAS was based on the question: *"How often do you drive faster than the speed limit on the motorway? (1) Never/rarely, (2) Sometimes, (3) Often, (4) Most of the time, (5) Do not drive on the motorway"*. The PGS that was based on the GWAS of the first principal component (PC) of the four risky behaviors (automobile speeding propensity, average number of drinks per week, ever smoker, lifetime number of sexual partners) was interpreted as capturing the general tendency to take risks across domains. And finally, the adventurousness GWAS was based on the question *"If forced to choose, would you consider yourself to be more cautious or more adventurous?" (1) Very cautious ... (5) Very adventurous* (Karlsson Linnér et al., 2019).

**Results**

The mean of the self-reported SPM score was 0.4 ($SD$ = 0.9), ranging from -2.6 to 3.4. Men scored significantly higher than women ($t$ = -7.45, $df$ = 3,556, $p$ < .001, effect size

Cohen's $d = 0.25$) and scores declined with participants' increasing age ($r = -.36$, $p < .001$). The correlation between the SPM and E5: Excitement-seeking was $r = .64$ ($p < .001$).

**The SPM as Predictor of Health- and Risk-Related Indicators.** First, we analyzed the associations of SPM with different health- and risk-related indicators. Results from correlation analyses in case of continuous variables and *t*-statistics in case of dummy-coded indicators are provided in tables S6.1 and S6.2 in supplemental materials. In order to find out, whether the SPM score is associated with the above-mentioned indicators also when the possible confounding effects of age and gender are taken into account, and whether these effects are comparable to those of E5: Excitement-seeking facet, we conducted a series of linear and logistic regression models. In these models, the eleven health- and risk-related variables were treated as outcomes, which were predicted by age and gender (in a baseline model) and SPM (Models 1) or the E5: Excitement-seeking facet (Models 2). In case of the continuous outcome variables (BMI, blood pressure, age at first alcohol consumption, total number of diagnosed diseases, and age at starting smoking regularly), linear regression models were run, and for binary outcome variables (experiencing anxiety/depression, having used drugs and/or smoked, having experienced traumatic injuries, and doing physical exercise), logistic regression models were conducted (for results, see Table 5). For each model, we report the unstandardized regression coefficient (with SE) and change in models' $F$- and $R^2$-statistics compared to the baseline.

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Insert Table 5 about here

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Findings demonstrate higher SPM score being associated with younger age at first alcohol consumption, older age at starting smoking regularly, smaller number of overall diseases diagnosed, smaller probability of feeling anxious or depressed, higher probability of doing physical exercise, and having experienced traumatic injuries. All these associations were statistically significant after controlling for age and gender. In comparison with the performance of E5: Excitement-seeking, the SPM score was far more successful in predicting anxiety or depression. Namely, higher SPM score was associated with significantly smaller probability of these mental health issues (*B* = -0.33, *SE* = 0.04, $\chi^2$ *change* = 61.93, $p < .001$, *Nagelkerke* $R^2$ *change* = .02). The E5: Excitement-seeking was also a significant predictor of experiencing anxiety/depression, but it explained a much smaller proportion of variance in this outcome ($\chi^2$ *change* = 6.84, $p < .01$, *Nagelkerke* $R^2$ *change* = .002), compared to the SPM. However, differently from the SPM, the E5: Excitement-seeking facet was statistically significantly associated to the probability having used or tried drugs (*B* = 0.04, *SE* = 0.02, $\chi^2$ *change* = 6.09, $p < .05$, *Nagelkerke* $R^2$ *change* = .005) and having smoked (*B* = 0.02, *SE* = 0.01, $\chi^2$ *change* = 9.78, $p < .01$, *Nagelkerke* $R^2$ *change* = .003). The SPM and the E5: Excitement-seeking scores were in a similar magnitude positively associated with the probability of doing physical exercise, and neither of the personality scores/scales was related to blood pressure or having been diagnosed with STDs (when age and gender were controlled for). In case of the SPM, there was a slight negative trend in predicting BMI, but this association was not statistically significant ($p = .08$).

**Polygenic Prediction of the SPM Score and the E5: Excitement-Seeking Facet.** In order to examine the genetic associations of the SPM and E5: Excitement-seeking in the Estonian Biobank cohort, we used seven PGSs – general risk tolerance, ever smoker, drinks per week, lifetime number of sexual partners, automobile speeding propensity, the first principal component of the four risky behaviors named above, and adventurousness – that were based on summary statistics from the respective meta-analysis of the GWAS reported in Karlsson Linnér and colleagues (2019). Correlations of personality scores to these seven PGSs can be found in supplemental materials (Table S7).

We analyzed the associations of SPM and E5: Excitement-seeking facets separately with each of these PGSs by creating a series of linear regression models (in R, function '*lm*'). In case of both personality phenotypes (the SPM and E5: Excitement-seeking), we first created a baseline regression model, where the phenotype was predicted by sex, age, and the top ten principal components of the cohort-specific genetic relatedness matrix. In the next step we then added one of the PGS (general risk tolerance, ever smoker, drinks per week, number of sexual partners, automobile speeding propensity, the first principal component of four risky behaviors, or adventurousness) to this baseline regression model. In Table 6 we report the *p*-values for the added PGS coefficients and the PGS-related increments in $R^2$ of the regression model compared with the baseline model. In Table 6 it can be seen that the self-reported SPM was significantly ($p < .05$) predicted by several risk-taking-related PGSs – general risk tolerance ($p = .005$), number of sexual partners ($p = .050$), automobile speeding ($p = .036$), first PC of risky behaviors ($p = .016$), and adventurousness ($p = .002$). The increment in adjusted $R^2$ was the largest in case of the PGSs 'adventurousness' and 'general risk tolerance', i.e., .002). Please note that these results were obtained using PGSs with no *p*-value threshold. In Table S8 in Supplemental Material it can be seen that when a somewhat more stringent *p*-value criterion is used for creating the PGSs ($p < .1$), the SPM is also associated with the 'ever smoker' PGS. However, the SPM is unrelated to the 'drinks per week' PGS. The E5: Excitement-seeking facet was significantly predicted by all the six PGSs ($p < .05$). The only PGS that did not significantly predict E5: Excitement-seeking was 'automobile speeding propensity' (when no *p*-value threshold was used). The increment in adjusted $R^2$ was the largest in case of the PGSs 'general risk tolerance' and 'the first PC of risky behaviors', i.e., .003).

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Insert Table 6 about here

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As an additional exploration we also tested whether the single NEO PI-3 item describing the enjoyment of risky situations (#172) could also be predicted by these seven risk-taking-related PGSs. The reason behind analyzing this item separately was that it had the largest weight in the SPM score in addition to being one of the eight items in the E5: Excitement-seeking facet. The association of the item #172 was the strongest with the PGS ‘general risk tolerance’ ($p < .001$; increment in adjusted $R^2$ was .003; see Table 6). The item #172 was also significantly ($p < .05$) predicted by the PGSs ‘ever smoker’, ‘the first PC of risky behaviors’, and the PGS ‘adventurousness’ (when PGSs were calculated using no *p*-value threshold).

## General Discussion

When we asked the skydivers, who participated in this research why they skydive, the most frequent answers were adrenaline rush, the feeling of freedom through freefall, exciting experience, pleasure, and great emotions. Data about having done a parachute jump is distinctive behavioral information that clearly distinguishes people from each other, drawing a line between individuals who have consciously taken a serious risk just for excitement and other intense positive feelings, and those who have not and most likely will never do so. Personality traits manifest in feelings, thoughts, and behaviors, but the latter is the only aspect of personality that can also be accessed more directly and can be thus externally validated. With this research we demonstrated that examining just a single behavioral act—skydiving—represents a useful and valid model of excitement-oriented risk-taking.

### Personality Profile of a Skydiver

Skydivers have a very distinctive personality profile. As expected, skydivers are excitement- and sensation-seekers. The finding of skydivers’ significantly lower Neuroticism as well as the more specific N1: Anxiety, N2: Angry hostility, N3: Depression, and N6: Vulnerability to stress facets scores is consistent with the view that sensation seekers are resilient to stress, which allows them to explore challenging environments laden with risks (Smith et al., 1992). Skydivers' higher levels of Openness, especially of O4: Actions and O6: Values, are also in agreement with previous studies about the associations between sensation seeking and FFM traits (Aluja et al., 2003; Roberti, 2004). In a nutshell, we demonstrated that at the level of personality facets skydivers are adventurous, curious, and energetic, calm under pressure, and open-minded, in addition to obviously seeking excitement. What is more, performing regularized regression analysis at the level of items revealed that the characteristics most strongly associated to skydiving belonged to the facets E5: Excitement-seeking (*enjoying risky situations*, #172) and to N5: Impulsivity (*being unable to resist cravings,* #51). To be clear, the latter had a negative association with being a skydiver. This finding implies that skydivers indeed take risks for excitement but not because of impulsivity.

The typical personality profile of a skydiver does not reveal that they would have major difficulties in experiencing and regulating their emotions (cf. Woodman et al., 2009). Although it may be tempting to think that individuals who engage with skydiving require extreme stimulation due to alexithymia and dampened emotional reactivity, our findings did not lend any support to this hypothesis. It can be seen in Figure 1 (see also Table S4.1 in supplemental materials) that skydivers did not show depressed O3: Openness to Feelings scores, relative to the norm group. Instead, skydivers appeared significantly more open to their feelings than demographically matched control individuals.

Nevertheless, it is also important to additionally examine other risky behaviors such as drug use for instance, as sensation seeking has also been found to be a vulnerability factor for different addiction disorders (Norbury & Husain, 2015). In Study 1, we showed that although skydivers did not have higher scores of N5: Impulsivity than the control group, they still exhibited relatively high levels of other forms of risk-taking such as having smoked or used drugs compared to the population-based sample of Study 2. However, this was most probably associated with their openness to different experiences, not with their problems with self-control. In Study 2 we demonstrated that the specific weighted combination of personality questionnaire items – the Skydiving Personality Markers or the SPM score – predicted health indicators and risky behaviors or their proxies also in a large population-based sample, demonstrating the robustness of these results. Our findings suggest that individuals in the large population-based sample who scored higher on the SPM tended to be more physically active and mentally healthier compared to low-scorers, but at the same time, had greater probability of having experienced traumatic injuries and an earlier onset of alcohol use. Thus, it seems that using this constructed personality score enabled us to detect “potential skydivers” from a larger normal-population-based sample.

Next, we examined the predictive ability of the SPM score in comparison with the E5: Excitement-seeking facet, which is a widely used risk-taking scale within the FFM framework. The aim of these analyses was to find out whether the SPM adds to the prediction of risk-related behaviors beyond E5: Excitement-seeking. In general, the newly constructed item risk score predicted several health- and risk-related indicators at least as effectively as E5: Excitement-seeking. The close associations between the two scores are of course not unexpected, as two items from the E5: Excitement-seeking facet were among the characteristics with largest weights in the SPM score. But we also found that the SPM is for some outcomes even more effective than the E5: Excitement-seeking. Although the E5 was associated to some risky behaviors such as the non-specific reports of having used drugs, the SPM was more strongly related to traumatic injuries and positive outcomes in terms of mental health (Study 2). For example, E5: Excitement-seeking but not the SPM significantly predicted the probability of ever being a smoker, but among those who had smoked, the higher SPM (but not E5) scores were associated with starting smoking regularly at a later age. This difference is quite surprising, as both scores include eight items from the NEO PI-3 and even have two items in common. Yet, the other six items of the SPM belong to other dimensions of the Big Five, not even to Extraversion. It is also important to note that half of the items of the E5: Excitement-seeking facet are probably not informative about risk proneness, because questions about watching horror movies, listening to loud music, and being in the crowd at sporting events are not very useful in studying the riskier side of excitement-seeking or even being active in a more general sense. It can be concluded that, in comparison with E5: Excitement-seeking, our SPM score had better predictive ability of the somewhat more functional risk-taking behavior, which may lead to traumatic injuries, but otherwise is less associated to negative consequences.

**Genetic Associations of Taking Risks to Feel Excitement**

A risky excitement and sensation seeking, which can lead to skydiving, seems to be a rather distinctive trait because in Study 1, only 19 genetic polymorphisms explained up to 9.5% of individual differences in this tendency. At a first glance, this is a surprisingly strong effect as we used a very short and not necessarily an optimal list of candidate SNPs. For comparison, in the studies of heritability, 10% is usually regarded a medium and 25% a large effect (Plomin, 2018, p. 43), and for psychological traits including intelligence PGS composed from hundreds of polymorphisms explain rarely more than 15% of variance (cf. Plomin, 2018). There is, however, a possibility that the result we obtained could be an overestimate due to potential model overfitting. Unfortunately, we were not able to validate the effects of these genetic polymorphisms in an independent population-based sample as was done in case of the personality poly-score in Study 2 – some of the significant genetic variants (e.g., the VNTR polymorphisms) were not represented on SNP chips and had to be specifically genotyped using restriction fragment length polymorphism analysis of PCR-amplified fragments.

It is widely acknowledged that sensation seeking behavior has a genetic basis, but there is still a lot of unclarity about specific genes and the neurobiological pathways through which they exert their effects (Munafò et al., 2003). Through a combination of case–control and polygenic score approach, we found some support to previous studies showing that genes related to the production or transportation of dopamine and serotonin are associated with personality and temperament (e.g., Benjamin et al., 2009; Ivorra et al., 2011; Kuhnen & Chiao, 2009; Vormfelde et al., 2006). For example, the SERT gene that showed the greatest tendency towards statistical significance in this study has been one of the prime candidate genes of personality from early days of personality genetics research (Munafò et al, 2003), and primary target of many efficacious antidepressant medications (Savitz & Ramesar, 2004). Our findings were, however, not significant enough to survive corrections of multiple testing.

Another potential explanation for the above-described findings is the complexity of the examined phenotype (cf. Boldak & Guszkowska, 2013). As already described above, our data show that even engaging in a rather specific and well-defined behavioral act such as skydiving differs from many other forms of excitement- and sensation-seeking: skydivers are not just prone to risk-taking but also emotionally stable, liberal, and adventurous, and thus exhibit traits across all FFM domains. As each personality trait is probably influenced by many genetic variants and gene–environment interactions (Van Gestel & Van Broeckhoven, 2003) and there are substantial differences even in the heritability of the specific facets of a single personality domain such as Neuroticism, for instance (Realo et al., 2017), we can only conclude that the expression of such a complex behavioral phenotype is most likely influenced by the effects of a vast number of gene variants, and that any polymorphism contributing to the phenotype is probably not sufficient to determine the trait (Kluger et al., 2002; Turkheimer et al., 2014). Our research thus highlights the importance of sound psychometric assessment of the excitement-seeking and other psychological phenotype(s). As pointed out by Montag and colleagues (2020) in a recent review, collaborative data sets that are often used in GWA studies typically include many phenotypes, which compromises the length of the measures of these phenotypes, and inevitably reduces the reliability of the assessment. Psychometric measurements usually require several items to capture a construct in depths and detail (Montag et al., 2020). However, the specificity of a single item can sometimes have its advantages. For instance, in our study, even the NEO PI-3 item #172 (*enjoying risky situations*) was statistically significantly predicted by the general risk tolerance PGS, which had been created using a similarly worded single item in the discovery GWAS (see Karlsson Linnér et al., 2019, and Table 6 of the present study). On the whole, supplementing self-reports with data about real world behavior is an advantageous solution for the problem of heterogeneity in psychometric assessment tools across different studies. As the effects of single genetic polymorphisms are very small when studying personality traits, precise measurement in order to reduce noise in data deserves serious consideration, and this is exactly why taking into account people's behavior may be helpful.

Here it should be acknowledged that the 'candidate gene' approach itself is limited in several ways (Hewitt, 2012)—among other things, by very small effects conferred by individual loci (Munafó & Flint, 2011), by still relatively small sample sizes (Karlsson Linnér et al., 2019), and by being constrained by the current level of neurobiological knowledge (Savitz & Ramesar, 2004). However, testing a larger number of SNPs lead to a large number of multiple comparisons and thus increased the false positive rates (Hong & Park, 2012). Thus, both approaches (GWAS and candidate genes) should play complimentary roles in examining the molecular genetics of personality and other phenotypes, but candidate gene studies must also be sufficiently powered and properly controlled (Montag et al., 2020). In case of the population-based cohort of Study 2 we decided to take advantage of the association results from previous large-scale GWA studies through analyzing risk-taking-related PGSs (meta-analyzed by Karlsson Linnér et al., 2019). Our results confirmed that individuals that were similar to skydivers in terms of specific personality markers were genetically distinguishable from the so-called classical sensation-seekers and risk-takers. The SPM score was unrelated to the PGS ‘drinks per week’ but was significantly predicted by the polygenic scores of ‘adventurousness’ and ‘automobile speeding propensity’, for instance. The E5: Excitement-seeking facet, on the other hand, was significantly predicted by the PGS ‘drinks per week’ among several other PGSs, but not to the speeding PGS. The E5: Excitement-seeking facet was also more robustly than the SPM score associated with the PGSs of some specific risky behaviors such as smoking and drinking. These findings suggest that the personality profile of skydiving may be linked to the genetics of adventurousness, which seems to be distinct from the so-called classical risk-taking and sensation-seeking. Skydiving behavior is comparable to automobile speeding as both incorporate finding pleasure in fast-paced motion, accompanied by the feeling of adrenaline rush, but driving faster than the speed limit is also associated to poor impulse control (Bıçaksız & Özkan, 2016), which is generally not common to skydivers. In sum, our findings indicate that skydivers’ personality phenotype is detectable from genetic variation and that examining both candidate gene polymorphisms and risk-related PGSs is more informative than focusing on only one approach. More broadly speaking, finding an optimal balance between increasing replicability of results, which is problematic in candidate gene studies (see Hirschhorn et al. 2002), and exploring causal associations between traits and genetic variants, which is problematic in GWA studies (see Montag et al., 2020), is one of the great challenges when examining the genetics of personality and other complex traits.

**Strengths and Limitations of our Study**

Our study has several strengths, one of them being an in-depth analysis of personality traits at different levels of specificity, in order to identify possible variation in skydivers' personality profiles that is beyond the excitement- or sensation-seeking traits. Another strength is that we examined several samples and followed two distinct approaches to analyzing genetic associations. The findings of this study may also make a practical contribution. Consistent with previous findings, our study has demonstrated that in addition to better mental health and greater physical fitness, risky excitement-seeking behavior is associated with higher probability of injuries and proneness to try different substances (Hopwood et al., 2007; Wingo et al., 2016). Accurate personality descriptions—such as provided by the SPM item risk score constructed and tested in this study—are key to targeting the individuals needing more attention (Frey et al., 2017), for instance those adolescents, whose personality scores of excitement-oriented risk-taking are extremely high.

However, some methodological limitations should also be noted. First, several health and risk indicators as well as personality data were collected using self-reports, which can be influenced by measurement bias. For example, recalling the age of initiation of alcohol use can easily be distorted (Livingston et al., 2016). Another widely known self-report-related measurement error – social desirability bias – could lead to underreporting some sensitive information (e.g., reports of STDs or using drugs; e.g., Crutzen & Göritz, 2020) and also influence answers to personality questionnaires, as people tend to respond to self-report items in a manner that makes them look good rather than in an accurate manner (e.g., Holtgraves, 2004). Fortunately, the heart of this research was an objectively measurable real behavioral act — a parachute jump. Second, it is important to note that although this study managed to explore some aspects of several important indicators that have previously been associated with seeking excitement and taking risks (such as extreme sports, drug use, smoking, drinking etc.), the list of health and risk markers used in present research was still rather limited in range, as sensation-seeking is known to have a large number of behavioral correlates (for review, see Roberti, 2004). Moreover, the behaviors or outcomes that were examined in this study (e.g., mental health or drug use) are multi-faceted in nature and should thus be ideally measured more comprehensively. And as for the third limitation, Study 1 was probably underpowered to detect small effects in polymorphisms with rare alleles, because a large sample size is needed even for simply observing a rare variant with a high probability. According to Lee and colleagues (2014), sampling an allele with a 0.5% frequency with 99% probability requires sequencing at least 460 individuals, even if perfect detection is assumed. The sample of 300 skydivers is relatively large for a small country with only about 1.3 million inhabitants but identifying small effects of rare variants would require even more cases and/or region- or gene-based multi-marker tests (Lee et al., 2014).

**Conclusions**

Our study demonstrated that skydivers have a distinctive personality profile. Enjoying risks, being emotionally stable, adventurous, and open-minded, but not impulsive seem to be the overall face of this kind of a risk-taker. We showed that a specific set of personality questionnaire items can be accurate in differentiating between individuals who have done a parachute jump and those who have not. Moreover, examining the same set of items when combined into an item risk score – the SPM – in a large population-based sample revealed that these characteristics had the ability to predict different health-related indicators. The SPM score was associated to greater physical activity, earlier onset of drinking alcohol, higher probability of traumatic injuries, and better mental health, and was also detectable from the polygenic scores of adventurousness, general risk tolerance, and automobile speeding. The SPM was, however, unrelated to the polygenic score associated with drinking alcohol. All in all, these findings seem to suggest to a distinctive — physically active and daring, but perhaps also more functional — type of excitement-seeking. Last but not least, our results provide some novel insight into the genetics of risky excitement-seeking, but as with most complex traits, more studies with larger samples and multiple methods are necessary to reach more conclusive outcomes.

## Data Accessibility Statement

The scripts and supplemental materials can be accessed here. The data of this study cannot be publicly shared due to legal and ethical restrictions. For access to the data please apply at https://genomics.ut.ee/en/biobank.ee/data-access.

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**Table 1**

*Review of Different Genetic Variants that have been related to Excitement- and Sensation Seeking Phenotypes in Earlier Studies using Candidate Gene Approach*

| Gene | Genetic variant / SNP | Phenotype | References |
|---|---|---|---|
| D4 receptor gene (DRD4) | Variable number of tandem repeats (VNTR) | Sensation seeking | Benjamin et al., 1996 |
| | | Novelty seeking | Ekelund, Lichtermann, Jarvelin, & Peltonen, 1999 |
| | | | Ptáček, Kuželová, H., & Stefano et al, 2011 |
| | | | Kluger, Siegfried, & Ebstein, 2002 |
| | | | Ono et al., 1997 |
| | | | Persson et al., 2000 |
| | | | Strobel, Wehr, Michel, & Brocke, 1999 |
| D2 receptor gene (DRD2) | rs1800497 or Taq1A[6] | Sensation seeking | Eisenberg, Campbell, MacKillop, Lum, & Wilson, 2007 |
| | | Impulsive behavior | Esposito-Smythers, Spirito, Rizzo, McGeary, & Knopik, 2009 |
| | | Novelty seeking | Keltikangas-Järvinen et al., 2009 |
| | | | Montag et al., 2010 |
| D3 receptor gene (DRD3) | rs167771 | Sensation seeking | Thomson, Carlson, & Rupert, 2013 |
| | | Autism spectrum disorders | Warrier, Chee, Smith, Chakrabarti, & Baron-Cohen, 2015 |
| Catechol-*O*-methyltransferase (COMT) gene | Valine158Methionine polymorphism (rs4680) | Impulsivity and addiction disorders | Benjamin, et al, 2000 |
| | | Extraversion | Kang, Song, Namkoong, & Kim, 2010 |
| | | Sensation seeking | Lang, Bajbouj, Sander, & Gallinat, 2007 |
| | | | Reuter & Hennig, 2005 |
| | | | Salo, Pulkki-Raback, Hintsanen, Lehtimaki, & Keltikangas-Jarvinen, 2010 |
| | | | Strobel, Lesch, Jatzke, Paetzold, & Brocke, 2003 |
| Dopa decarboxylase (DDC) gene | rs12669770 and rs11575543 | Sensation seeking | Derringer, Krueger, Dick, Saccone, Grucza, Agrawal, et al, 2010 |
| | | | Norbury & Husain, 2015 |
| GTP cyclohydrolase 1 (GCH1) gene | rs841 | Novelty seeking | Sadahiro et al., 2011 |
| Serotonin transporter (SERT) gene | Serotonin transporter gene-linked polymorphic region (SERTPR) | Novelty seeking | Heils, Teufel, Petri, Stöber, Riederer, Bengel, et al, 1996 |
| | | Anxiety | Strobel et al., 2003 |
| | | | Vormfelde et al., 2006 |
| SERT gene | Intron 2 (STin2) VNTR polymorphism | Novelty seeking | Vormfelde et al., 2006 |
| | | Anxiety | |

| | | | |
|---|---|---|---|
| SERT gene | rs25531 | Neuroticism | Chang, Chang, Fang, Chang, & Huang, 2017 |
| Serotonin 2A (HT2A) receptor gene | rs6313 | Novelty seeking | Heck et al, 2009 |
| Serotonin 2B (HT2B) receptor gene | rs6437000, rs10194776, rs1549339 | Fun seeking (in behavioral activation system) | Zhu et al., 2012 |
| Androgen receptor (AR) gene | Polymorphic trinucleotide repeats CAG and GGN | Extraversion | Aluja, Garcia, Blanch, & Fibla, 2011 |
| | | Impulsivity | Vermeersch, T'Sjoen, Kaufman, Vincke, & Van Houtte, 2010 |
| | | Mood | Westberg et al., 2009 |
| Cholinergic receptor muscarinic 2 (CHRM2) gene | rs7800170 and rs1824024 | Disinhibition (sensation seeking) | Dick et al., 2008 |
| | | | Hendershot, Bryan, Ewing, Claus, & Hutchison, 2011 |
| Brain-derived neurotrophic factor (BDNF) gene | Valine66Methionine polymorphism or rs6265 | Novelty seeking | Montag et al., 2010 |
| | | Harm avoidance | Kang et al,, 2010 |
| | | Boredom susceptibility (sensation seeking) | |
| Catenin (cadherin-associated protein) alpha 2 (CTNNA2) gene[7] | rs7600563 | Excitement-seeking | Terracciano et al., 2011 |

**Table 2**

*Descriptive Statistics of Skydivers and Demographically Matched Controls*

| Demographics | Skydivers | Controls |
|---|---|---|
| Sample size | 298 | 298 |
| Sex, % (*n*) | | |
| Male | 65 (194) | 65 (195) |
| Female | 35 (104) | 35 (103) |
| Age | | |
| Range | 16-69 | 18-69 |
| Mean (*SD*) | 32.4 (7.9) | 32.5 (7.9) |
| Education, % (*n*) | | |
| Compulsory | 1 (4) | 1 (3) |
| General Secondary | 21 (63) | 21 (61) |
| Vocational Secondary | 18 (53) | 19 (57) |
| Higher | 60 (178) | 59 (177) |

**Table 3**

*Comparison of SPM and E5: Excitement-Seeking as Predictors of Health- and Risk-Related Indicators in the Sample of Skydivers*

| | *Models I:* SPM as predictor | | | *Models II:* E5 as predictor | | |
|---|---|---|---|---|---|---|
| *Linear Regression Models* | Coefficient | Change compared to the baseline model[a] | | Coefficient | Change compared to the baseline model[a] | |
| | *Beta (SE)* | Incremental *F* | Incremental adjusted $R^2$ | *Beta (SE)* | Incremental *F* | Incremental adjusted $R^2$ |
| Body mass index | 0.09 (0.23) | 0.17 (*n.s.*) | <.001 | 0.05 (0.04) | 1.46 (*n.s.*) | .001 |
| Parachute jumps | 59.18 (24.04) | 6.06* | .016 | -4.49 (4.04) | 1.23 (*n.s.*) | .001 |
| | *Models I:* SPM as predictor | | | *Models II:* E5 as predictor | | |
| *Binary Logistic Regression Models* | *Beta (SE)* | Incremental $\chi^2$ | Incremental *Nagelkerke* $R^2$ | *Beta (SE)* | Incremental $\chi^2$ | Incremental *Nagelkerke* $R^2$ |
| Traumatic injuries (1/0) | 0.29 (0.16) | 0.78 (*n.s.*) | .014 | 0.01 (0.03) | 0.03 (*n.s.*) | < .001 |
| Skydiving injuries (1/0) | 0.48 (0.19) | 1.30** | .033 | -0.04 (0.03) | 0.28 (*n.s.*) | .007 |
| Smoking (1/0) | 0.33 (0.16) | 1.03* | .019 | 0.08 (0.03) | 2.12** | .039 |
| Drug use (1/0) | 0.33 (.16) | 1.02* | .018 | 0.07 (0.03) | 1.44* | .026 |
| Extreme sports (1/0) | 0.43 (0.16) | 1.71** | .031 | 0.06 (0.03) | 1.43* | .026 |
| Physical exercise (1/0) | 0.21 (0.20) | 0.16 (*n.s.*) | .006 | 0.03 (0.03) | 0.08 (*n.s.*) | .003 |

*Note.* ** $p < .01$; * $p > .05$; *n.s.* = statistically non-significant ($p > .05$); $N = 298$. [a] Regression with only age and gender as predictors of the (either continuous or binary) outcome (body mass index, number of parachute jumps, general traumatic injuries, skydiving-related injuries, smoking, drug use, extreme sports participation besides skydiving, and doing physical exercise).

**Table 4**

*Predicting Skydiving from Literature-Proposed Genetic Variants (Binary Logistic Regression)*

| | Gene | Coefficient | Standard Error | Wald *Z* | *p*-value | Odds Ratio (95% CI) | Change in Nagelkerke $R^{2\,*}$ |
|---|---|---|---|---|---|---|---|
| Intercept | | 1.12 | 0.68 | 1.66 | .097 | | |
| Gender | | 0.04 | 0.21 | 0.17 | .862 | 1.04 (0.69; 1.56) | |
| Age | | 0.02 | 0.01 | 1.53 | .125 | 1.02 (1.00; 1.05) | |
| GGN | AR | -0.11 | 0.12 | -0.94 | .345 | 0.90 (0.71; 1.13) | .001 |
| CAG | AR | -0.14 | 0.11 | -1.29 | .197 | 0.87 (0.70; 1.08) | .007 |
| SERTPR vntr | SERT | -0.41 | 0.16 | **-2.48** | **.013** | 0.67 (0.48; 0.92) | .009 |
| DRD4 vntr | DRD4 | -0.20 | 0.18 | -1.09 | .277 | 0.82 (0.57; 1.17) | .003 |
| STin2 vntr | SERT | -0.27 | 0.16 | -1.72 | .086 | 0.76 (0.56; 1.04) | .001 |
| rs6437000 | HTR2B | -0.36 | 0.44 | -0.83 | .409 | 0.70 (0.29; 1.65) | .000 |
| rs10194776 | HTR2B | -0.27 | 0.36 | -0.75 | .455 | 0.76 (0.37; 1.55) | .000 |
| rs1549339 | HTR2B | 0.50 | 0.56 | 0.90 | .370 | 1.65 (0.55; 5.00) | .000 |
| rs167771 | DRD3 | -0.48 | 0.21 | **-2.31** | **.021** | 0.62 (0.41; 0.93) | .008 |
| rs11575543 | DDC | -0.56 | 0.46 | -1.24 | .216 | 0.57 (0.23; 1.37) | .008 |
| rs12669770 | DDC | -0.25 | 0.15 | -1.69 | .091 | 0.78 (0.59; 1.04) | .007 |
| rs7800170 | CHRM2 | -0.02 | 0.17 | -0.10 | .921 | 0.98 (0.70; 1.37) | .001 |
| rs1824024 | CHRM2 | -0.03 | 0.19 | -0.15 | .884 | 0.97 (0.67; 1.41) | .000 |
| rs6265 | BDNF | 0.23 | 0.20 | 1.17 | .242 | 1.26 (0.86; 1.85) | .002 |
| rs1800497 | ANKK1 | -0.03 | 0.18 | -0.14 | .889 | 0.98 (0.69; 1.38) | .000 |
| rs6313 | HTR2A | 0.15 | 0.15 | 1.01 | .311 | 1.17 (0.87; 1.57) | .003 |
| rs841 | GCH1 | -0.40 | 0.19 | **-2.11** | **.035** | 0.67 (0.46; 0.97) | .005 |
| rs25531 | SERT | -0.54 | 0.28 | **-1.91** | **.056** | 0.58 (0.33; 1.01) | .012 |
| rs4680 | COMT | -0.19 | 0.14 | -1.33 | .182 | 0.83 (0.62; 1.09) | .004 |
| Nagelkerke $R^2$ = .095 | | | | | | | |
| Chi-square of model = 34.61, *df* = 21, $p < .05$ | | | | | | | |
| Percentage correctly classified = 63.6% | | | | | | | |

*Note.* Results shown in bold are significant ($p < .05$) predictors of being a skydiver or indicate a statistical trend ($p = .056$); CI = confidence interval. * Change in Nagelkerke $R^2$ compared to a baseline model where skydiving is predicted by age and gender; calculated for logistic regression models where each genetic variant was modelled separately as a single predictor of skydiving.

**Table 5**

*Comparison of SPM and E5: Excitement-Seeking Scores as Predictors of Health- and Risk-Taking-Related Indicators in a Population-Based Sample of 3,558 Individuals*

| *Linear Regression Models* | Models I: SPM as predictor | | | Models II: E5 as predictor | | |
|---|---|---|---|---|---|---|
| | Coefficient | Change compared to baseline model [a] | | Coefficient | Change compared to baseline model [a] | |
| | *Beta (SE)* | Incremental *F* | Incremental $R^2$ | *Beta (SE)* | Incremental *F* | Incremental $R^2$ |
| Body mass index | -.15 (.09) | 3.09 | .001 | .00 (.02) | 0.04 | .000 |
| Blood pressure (systolic) | -.20 (.30) | 0.43 | .000 | .07 (.05) | 1.69 | .000 |
| Age at first alcohol consumption | -.16 (.06) | 6.71** | .002 | -.04 (.01) | 14.42*** | .004 |
| Age at starting smoking regularly | .33 (.15) | 5.27* | .003 | .01 (.03) | 0.20 | .000 |
| Number of diseases | -.32 (.11) | 8.15** | .002 | -.05 (.02) | 7.17** | .002 |

| *Binary Logistic Regression Models* | Models I: SPM as predictor | | | Models II: E5 as predictor | | |
|---|---|---|---|---|---|---|
| | *Beta (SE)* | Incremental $\chi^2$ | Incremental *Nagelkerke* $R^2$ | *Beta (SE)* | Incremental $\chi^2$ | Incremental *Nagelkerke* $R^2$ |
| Anxiety/depression (0/1) | -.33 (.04) | 61.93*** | .024 | -.02 (.01) | 6.84** | .002 |
| Physical exercise (0/1) | .37 (.06) | 44.95*** | .023 | .06 (.01) | 48.75*** | .024 |
| Drug use (0/1) | .08 (.10) | 0.66 | .000 | .04 (.02) | 6.09* | .005 |
| Injuries/poisonings (0/1) | .24 (.06) | 14.50*** | .008 | .02 (.01) | 5.03** | .003 |
| STDs (0/1) | .03 (.08) | 0.17 | .001 | .01 (.01) | 0.20 | .000 |
| Having smoked (0/1) | -.02 (.04) | 0.17 | .000 | .02 (.01) | 9.78** | .003 |

*Note.* * $p < .05$, ** $p < .01$, *** $p < .001$. [a] Regression with only age and gender as predictors of the outcome. STDs = sexually transmitted diseases.

**Table 6**

*Personality Phenotypes Predicted by Polygenic Scores (PGS) Calculated on basis of the Association Results from Karlsson Linnér et alas (2019)*

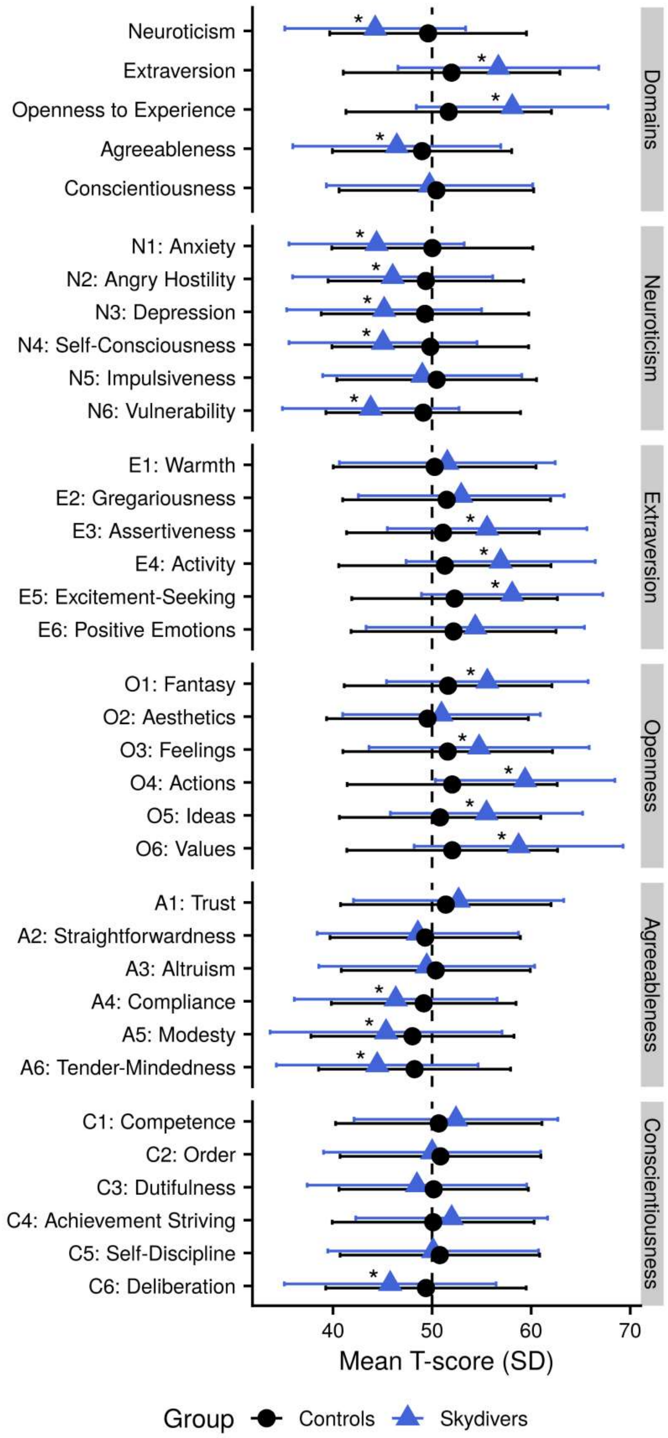
| *Polygenic score (PGS) as predictor* | GWAS sample size [a] | SPM score as outcome | | E5: Excitement-seeking as outcome | | #172 (*enjoying risky situations*) as outcome | |
|---|---|---|---|---|---|---|---|
| | | *P*-value for the PGS coefficient | Incremental [b] adjusted $R^2$ | *P*-value for the PGS coefficient | Incremental[b] adjusted $R^2$ | *P*-value for the PGS coefficient | Incremental[b] adjusted $R^2$ |
| General risk tolerance[1] | 975,353 | **.005** | .0017 | **.000** | .0029 | **.000** | .0030 |
| Ever been smoker or not[2] | 518,633 | .145 | .0003 | **.005** | .0015 | **.006** | .0017 |
| Average number of drinks consumed per week | 414,291 | .426 | .0000 | **.012** | .0012 | .303 | .0000 |
| Lifetime number of sexual partners[3] | 370,711 | **.050** | .0007 | **.013** | .0011 | .137 | .0003 |
| Automobile speeding propensity[4] | 404,291 | **.036** | .0008 | .178 | .0002 | .108 | .0004 |
| The first PC of risky behaviors[5] | 315,894 | **.016** | .0012 | **.000** | .0026 | **.007** | .0016 |
| Adventurousness[6] | 557,923 | **.002** | .0021 | **.003** | .0016 | **.011** | .0014 |

*Note.* [a] from Karlsson Linnér et al. (2019; Table 1); [b] Compared to a baseline linear regression model, where the phenotype was predicted by sex, age, and the top ten principal components of the cohort-specific genetic relatedness matrix; PC = principal component; SPM = Skydiving Personality Markers. *P*-values of PGS coefficients shown in bold are statistically significant ($p < .05$). PGSs were calculated for the Estonian Biobank cohort on basis of genome-wide association studies' results meta-analyzed by Karlsson Linnér and co-authors (2019) using no *p*-value threshold (i.e., $p = 1$). Associations with different *p*-value thresholds (i.e., $p = .0001$, $p = .001$, $p = .01$, $p = .05$, $p = .1$, and $p = .5$) can be found in Supplemental Materials, Table S8. In these GWA studies, the seven phenotypes were coded such that higher phenotype values were associated with higher risk tolerance or risk taking. [1] Based on the question "*Would you describe yourself as someone who takes risks? (Yes / No)"* in the UKB sample and *"In general, people often face risks when making financial, career, or other life decisions. Overall, do you feel comfortable or uncomfortable taking risks?" (Very comfortable ... Very uncomfortable)* in the 23andMe sample; [2] Coded as 1 if a respondent reported being a current or previous smoker and 0 if they reported never smoking or only smoking once or twice. [3] Based on the question: *"About how many sexual partners have you had in your lifetime?";* [4] Based on the question: *"How often do you drive faster than the speed limit on the motorway? (Never/rarely ... Most of the time);* [5] Based on the GWAS of the first principal component (PC) of the four risky behaviors (automobile speeding propensity, average number of drinks per week, ever smoker, lifetime number of sexual partners); [6] Based on the question *"If forced to choose, would you consider yourself to be more cautious or more adventurous?"* (*Very cautious ... Very adventurous).*

**Figure Captions**

*Figure 1.* *T*-scores (with standard deviations) of NEO Personality Inventory-3 (NEO PI-3) domain and facet scales for skydivers and matched controls. Blue triangles indicate the mean scores of skydivers; black circles show the means of individuals in the control group. Facets are grouped by the domain they define: N1 to N6 = facets of Neuroticism, E1 to E6 = facets of Extraversion, O1 to O6 = facets of Openness to Experience, A1 to A6 = facets of agreeableness, and C1 to C6 = facets of Conscientiousness. An asterisk (*) indicates significant differences ($p > .05$) between the two groups. Domain and facet scores of skydivers and controls were standardized into *T*-scores relative to the NEO PI-3 means in the population-based sample of the Estonian Genome Center at the University of Tartu ($N$ = 3,603).

**Figure 1**


Neuroticism
Extraversion
Openness to Experience
Agreeableness
Conscientiousness
Domains
N1: Anxiety
N2: Angry Hostility
N3: Depression
N4: Self-Consciousness
N5: Impulsiveness
N6: Vulnerability
Neuroticism
E1: Warmth
E2: Gregariousness
E3: Assertiveness
E4: Activity
E5: Excitement-Seeking
E6: Positive Emotions
Extraversion
O1: Fantasy
O2: Aesthetics
O3: Feelings
O4: Actions
O5: Ideas
O6: Values
Openness
A1: Trust
A2: Straightforwardness
A3: Altruism
A4: Compliance
A5: Modesty
A6: Tender-Mindedness
Agreeableness
C1: Competence
C2: Order
C3: Dutifulness
C4: Achievement Striving
C5: Self-Discipline
C6: Deliberation
Conscientiousness
40
50
60
70
Mean T-score (SD)
Group
Controls
Skydivers

**Footnotes**

[1] In addition to the yes/no answer, skydivers were asked to specify the type(s) of psychotropic substance(s) they have used/tried. Most participants reported having used marijuana (cannabis), but altogether 34 skydivers specified that they had additionally tried/used different psychostimulant drugs such as amphetamine, MDMA, and cocaine. There were fewer reports of having tried hallucinogenic substances such as LSD or psychoactive fungi). Altogether 16 skydivers did not specify the type of drug they have tried.

[2] The mix consisted of 8uL Hi-Di formamide, 0.5uL ROX500, and 1.5uL undiluted DNA (0.5uL HEX, 0.5uL TAMRA, 0.5uL FAM).

[3] This is one of the very few items that is worded differently in the Estonian version of the NEO PI-3 compared to the original English version of the questionnaire (#172: *enjoying the excitement of roller coasters*).

[4] The theoretical minimum value of the SPM (i.e., in case someone would have rated all items with negative weights as ‘4’, and all items with positive weights as ‘0’) was -2.61, and the theoretically highest possible value (in case all items with positive weights would have been rated ‘4’, and all items with negative weights as ‘0’) was 3.70.

[5] In order to benchmark this result against a null model, we conducted an additional exploration, using simulated SNP data. We used function *‘simulateSNPglm’* (package *‘scrime’*, version 1.3.5; Schwender & Fritz, 2018) in R environment (R Core Team, 2013) to generate the SNPs and ran logistic regression models with similar parameters as was done in the original candidate gene analysis of this study. More specifically, we used the same dependent variable (skydiver = 1 *versus* control = 0; sample size $n$ = 596), which was predicted by simulated SNPs ($n$ = 19) with the same minor allele frequencies (MAFs) as the actual candidate gene variants in Study 1. We repeated this regression model (each time with different set of 19 simulated SNPs with the same MAFs) for 1,000 times. The average

Nagelkerke $R^2$ of all these models was 0.042 (*SD* = 0.013; 99% CI [0.041; 0.044]). This means that the probability of a result randomly (but under similar parameters) being as high or higher than 0.095 is about 0.0002.

[6] The Taq1A was originally associated with the DRD2 gene, but was later found to be located within the adjacent gene, the Ankyrin repeat and kinase domain containing 1 or ANKK1. It is nevertheless involved in controlling the synthesis of dopamine in the brain (NCBI Gene).

[7] Unfortunately, the SNP rs7600563 in CTNNA2 was not represented on the HumanCoreExome BeadChip that was used to genotype the sample of skydivers. Although this SNP was genotyped separately for the group of skydivers (and imputed for the controls), genotyping was unsuccessful for almost half of the skydivers (*n* = 135), which is why rs7600563 was omitted from the logistic regression model (predicting being a skydiver) and thus also from the polygenic score. (We analyzed the differences in rs7600563 between the remaining 163 skydivers and matching control individuals and found no significant differences.)