Published in final edited form as:

Biol Psychol. 2019 April ; 143: 93–102. doi:10.1016/j.biopsycho.2019.02.012.

Putting the flight in “fight-or-flight”: Testosterone reactivity to skydiving is modulated by autonomic activation

Stuart F. White^{a,1}, Yoojin Lee^{b,1}, Jenny M. Phan^b, Shannin N. Moody^b, and Elizabeth A. Shirtcliff^{b,*}

^aCenter for Neurobehavioral Research, Boys Town National Research Hospital, 14100 Crawford Street, Boys Town, NE 68010, USA

^bDepartment of Human Development and Family Studies, 2361C Palmer, 2222 Osborn Dr, Ames, IA 50011, USA

Abstract

Sensation-seeking (SS) involves the tendency to pursue exciting activities, potentially including risky behaviors (e.g., substance use, risky sexual behavior). Testosterone is associated with cortisol, SS, and autonomic nervous system (ANS) functioning. Testosterone reactivity/recovery during sky-diving and its relationship to cortisol response, ANS response and SS were examined. Forty-four participants provided reactive saliva samples and autonomic activity data before, during and after sky-diving and as well as basal day saliva samples. Testosterone reactivity/recovery to skydiving was significantly greater than basal day measurements. Testosterone re- sponsivity to skydiving was predicted by increased cortisol, increased sympathetic activity (heart rate) and reduced parasympathetic activity (RMSSD). Independent of physiological effects, increased SS predicted testosterone responsivity to skydiving. These data suggest that testosterone reactivity, and its relationship to ANS responsivity, may be associated with pleasurable responses to risky/ intense situations. These data may be useful in developing novel intervention strategies for risky behaviors.

Keywords

Testosterone; Sensation-seeking; Skydiving; Autonomic nervous system

1. Introduction

Sensation-seeking (SS) is a personality trait describing an affinity for novel, intense and exciting experiences and a willingness to take risks in order to facilitate exhilarating experiences (Zuckerman, 1990). Individuals endorsing high SS levels are more likely to participate in highrisk activities, such as dangerous sports and jobs (Freixanet, 1999; Musolino & Hershenson, 1977; Thronquist, Zuckerman, & Exline, 1991). Critically, high levels of SS are associated with negative outcomes, such as substance-abuse (Stautz & Cooper, 2013), risky sexual behavior (Charnigo et al., 2013) and antisocial behavior (Mann

*Corresponding author. birdie@iastate.edu (E.A. Shirtcliff).

¹Note: The first and second authors contributed equally to this paper.

et al., 2017; Wilson & Scarpa, 2014). However, the role of psychobiological mechanisms, especially testosterone, and autonomic nervous system (ANS) functioning, in the association between SS and these outcomes is unclear and understudied. How individuals frame and cope with stressful experiences is thought to contribute to the emotional experiences of these actions (Lazarus, 2006). Understanding the role of, and individual differences in, psychobiological mechanisms in the response to intense or stressful situations may be useful in reducing negative outcomes associated with SS.

Skydiving is a quintessential SS activity. Despite substantially lower risk of mortality compared to commonplace activities such as driving (Hart, Griffith, & Randell, 2006), skydiving generates a substantial physiological response. Skydiving has been associated with increased epinephrine (Richter et al., 1996), norepinephrine (Richter et al., 1996), alpha-amylase (Chatterton, Vogelsong, Lu, & Hudgens, 1997), prolactin (Chatterton et al., 1997; Richter et al., 1996), and growth hormone levels (Chatterton et al., 1997; Richter et al., 1996). Moreover, leaping from an airplane in flight also produces an autonomic nervous system response (Allison et al., 2012; Richter et al., 1996) and increased cortisol reactivity (Chatterton et al., 1997; Hare, Wetherell, & Smith, 2013; Meyer et al., 2015; Richter et al., 1996). Thus, skydiving is an excellent way to understand the role of psychobiology in SS in an acute real-world context.

Surprisingly, testosterone response to skydiving has been neglected in the literature. Testosterone is a hormone with anabolic and androgenic functions that induces dramatic masculinizing changes to the body, especially during sensitive periods (Arnold & Breedlove, 1985). Testosterone is also thought to modulate a number of social processes, including SS. Increased basal testosterone is associated with increased trait SS (Campbell et al., 2010). Moreover, there is evidence that testosterone level can change dramatically in an acute context (testosterone reactivity), which helps the individual to better adapt to an environmental context (Archer, 2006). In competitive situations, successful performance is followed by an increase in testosterone (e.g., Apicella, Dreber, & Mollerstrom, 2014; Booth, Shelley, Mazur, Tharp, & Kittok, 1989; Coates & Herbert, 2008; Hasegawa, Toda, & Morimoto, 2008). In contrast, increased parental investment in new fathers is associated with *decreased* testosterone levels, as well as SS (Perini, Ditzen, Hengartner, & Ehlert, 2012). Interestingly, the single study examining testosterone and skydiving found that jumping was associated with a *decrease* in testosterone (Chatterton et al., 1997). However, basal testosterone levels were assessed in the morning and skydiving took place in the afternoon. Testosterone has a known diurnal rhythm whereas it decreases across the course of the day (Khan-Dawood, Choe, & Dawood, 1984; Plymate, Tenover, & Bremner, 1989). As this was not adequately addressed in the Chatterton study, the results are difficult to interpret. Thus, testosterone has still not been adequately examined in a genuinely thrilling (as opposed to stressful) context, like recreational skydiving.

Given that prior studies have viewed skydiving as a stressor, it may also be fruitful to examine testosterone reactivity in concert with stress biomarkers such as cortisol and autonomic activation. There is substantial interaction and communication across the hypothalamic-pituitary-adrenal (HPA) and hypothalamic-pituitary-gonadal (HPG) axes (Viau, 2002) with potentially important implications for negative behaviors, such as mental

illness (Marceau, Ruttle, Shirtcliff, Essex, & Susman, 2015). Two emerging theories lend toward distinct predictions for how testosterone and cortisol should interact. A dual-axis view purports that behavioral effects of testosterone are dominant when cortisol levels are low (Carré & Mehta, 2011; Mehta, Jones, & Josephs, 2008; Mehta, Welker, Zilioli, & Carré, 2015; Mehta & Josephs, 2010). When a situation is viewed as threatening/stressful cortisol reactivity is dominant, whereas a testosterone response will be seen when a situation is viewed as challenging (Wobber et al., 2010). According to this dual-axis view, because SS traits reflect a tendency to view novel and intense situations as challenging rather than stressful or threatening, individuals with high SS and low cortisol are hypothesized to have the largest testosterone response to the thrill of skydiving. Ours' (Meyer et al., 2015) and others' (Chatterton et al., 1997; Hare et al., 2013; Meyer et al., 2015; Richter et al., 1996) findings for cortisol reactivity in response to skydiving challenges this dual-axis view. An alternative theory suggests that situations that are both stressful and challenging, such as skydiving, will elicit HPA-HPG co-activation and thus increase both cortisol and testosterone response (Shirtcliff et al., 2015). This coupling theory predicts that individuals with higher cortisol or greater cortisol reactivity to skydiving would also demonstrate the greatest testosterone reactivity as thrills are exciting precisely because they are both stressful and challenging.

This view about coupling of stressful and challenging contexts may extend to other stress biomarkers. Both testosterone and SS are also associated with ANS functioning, yet it is surprisingly rare for these biomarkers to be examined together. Testosterone has been observed to be positively associated with parasympathetic nervous system response (Do ru, Ba ar, Yuvanç, Sim ek, & Sahin, 2010; Ermis et al., 2010; Wranicz et al., 2004) and, in at least one study, negatively associated with sympathetic nervous system functioning (Do ru et al., 2010). Notably, however, these studies were conducted in cardiac (Do ru et al., 2010; Wranicz et al., 2004) and hypo-gonadal patients (Ermis et al., 2010), raising concerns about generalizability. In a sample of healthy adults, lower resting respiratory sinus arrhythmia, indicative of lower parasympathetic activation, was associated with increased testosterone reactivity (E. C. Porges, Smith, & Decety, 2015). In our previous work using data from the current sample, SS was associated with dual activation of the parasympathetic and sympathetic nervous systems leading up to the skydiving jump (Allison et al., 2012). Dual activation of the parasympathetic and sympathetic nervous systems is associated with intensely pleasurable activities theoretically (Beauchaine, 2001). Indeed, activities ranging from ejaculation (Kandeel, Koussa, & Swerdloff, 2001) to sauna baths (Radtke et al., 2016) stimulate dual activation of the two autonomic branches. Despite testosterone's relationship to SS (Campbell et al., 2010) and ANS functioning (e.g., Porges et al., 2015), it is not clear whether ANS functioning has a role in modulating testosterone response to skydiving, nor whether the relationship between testosterone and ANS functioning is independent of SS. It is possible that the experience of a physiological "rush" in response to a thrilling context would account for SS. That physiological "rush" might consist of the dual activation of the parasympathetic and sympathetic nervous systems, an increase in testosterone, or both.

Finally, gender should be considered with respect to testosterone, SS and skydiving. Both males and females produce testosterone, but there are gender differences. Testosterone is largely of gonadal origin in males, but of both ovarian and adrenal origin in females

(Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004; Shirtcliff, Granger, & Likos, 2002). Beginning with puberty, males produce more testosterone than females so that, by adulthood, levels are substantially higher in males (Granger et al., 2003; Shirtcliff, Dahl, & Pollak, 2009). Testosterone appears to be most reactive to masculine-type contexts, such as competition and dominance contests (Archer, 2006). Despite these gender differences, some studies have found that, within women, testosterone is responsive to challenge (Bateup, Booth, Shirtcliff, & Granger, 2002; Casto, Rivell, & Edwards, 2017; Edwards & Casto, 2013), particularly if the female participants won a competition (Oliveira, Gouveia, & Oliveira, 2009). Similar patterns of testosterone reactivity for males and females have been reported (e.g., Crewther, Obminski, & Cook, 2016; Jiménez, Aguilar, & Alvero-Cruz, 2012), although the more consistent finding is that testosterone responses to challenge and competition is more pronounced in males compared to females (Carré, Campbell, Lozoya, Goetz, & Welker, 2013; Kivlighan, Granger, & Booth, 2005) and that the behavioral implications of testosterone reactivity is different for males and females (Crewther et al., 2016; Geniole, Busseri, & McCormick, 2013; Schultheiss, Wirth, & Stanton, 2004). Gender differences in testosterone reactivity to skydiving have not been investigated, but it is reasonable to predict that males will be more reactive given that testosterone may be more reactive to challenging contexts in males (Carré et al., 2013; Kivlighan et al., 2005) and skydiving may be conceptualized as a masculine-context given that skydiving is more common in males than females, and even within skydivers, female skydivers perceive more risks associated with jumping than males (Green, Turner, Purdie, & McClure, 2003).

The current study examined testosterone reactivity during skydiving, relative to a basal (no jump) day. Furthermore, cortisol and ANS data was acquired before, during and after the jump. The goal of the study was to examine the relationship between SS and testosterone reactivity and the degree to which that relationship is modulated by cortisol and ANS response. Four hypotheses were made. First, greater testosterone response would be observed on the jump day relative to the basal day, and gender differences in testosterone responsivity are hypothesized. Second, increased testosterone responsivity was hypothesized to be associated with greater sensation-seeking. Third, consistent with the idea that HPA and HPG axes will both be activated during a challenging and stressful activity and studies that find cortisol reactivity to skydiving, it was predicted that greater cortisol response would be associated with greater testosterone response. We examined whether cortisol accounted for the relationship between SS and testosterone but were agnostic about whether these moderators of testosterone reactivity were independent. Fourth, in previous work in this sample (Allison et al., 2012), dual activation of the parasympathetic and sympathetic nervous systems was observed. Therefore, it was hypothesized that ANS activation, particularly dual activation of the parasympathetic and sympathetic nervous systems, would modulate testosterone reactivity to skydiving and might account for the relationship between SS and testosterone responsivity.

2. Methods

2.1. Participants

Forty-four participants were recruited at a recreational skydiving company. Participants were adults between 18 and 50 who were willing and capable of skydiving. The sample was 72.7% male ($n = 32$) and 90.9% Caucasian ($n = 40$). Experienced skydivers (34.1%, $n = 15$) had completed a median number of 208 previous jumps (range 23–8000), and all others were first-time jumpers. Measurement of the ANS was missing for 18% of the sample ($n = 8$) due to erroneous electrode application or interference from chest hair. The proportion of participants with complete autonomic versus missing data did not significantly differ in terms of group [i.e., novice or experienced skydiver; $\chi^2 = .051$, $p = .822$], race/ethnicity [$\chi^2 = .978$, $p = .613$], or gender [$\chi^2 = .025$, $p = .873$]. The groups with and without ANS data also did not significantly differ on average age [$t(42) = 1.04$, $p = .303$], BMI [$t(42) = 1.486$, $p = .145$], and SS ratings [$t(42) = .728$, $p = .471$] (see Table 1). Participants were excluded if they were unwilling to complete the training provided by the skydiving company. The research protocol was approved by the Institutional Review Board at the University of New Orleans.

2.2. Procedures

In order to minimize the impact of circadian rhythmicity on testosterone levels, participants arrived at the skydiving site in the early afternoon, approximately 90 min before skydiving [mean_{pre-jump} = 91.87 min (SD = 34.46 min)]. Participants were provided detailed information about the project, provided informed consent, and then provided the first saliva sample. To measure ANS response from participants, an Actiheart device was applied. The battery-powered electrodes were placed horizontally on the left chest, approximately three inches away from each other and two inches from the arm crevice. Participants without prior skydiving experience then completed ten minutes of the instruction for skydiving. Both novice and experienced skydivers then provided a second saliva sample before boarding the airplane [mean_{post-jump} = 26.97 min (SD = 5.70)]. Participants then ascended to 14,000 ft, and jumped from the airplane. The free-fall period was approximately 1.5 min and parachute gliding lasted approximately 4.5 min. A third saliva sample was provided immediately after landing [mean_{post-jump} = 7.91 min (SD = 4.77)] and a fourth saliva sample was provided fifteen minutes after landing [mean_{post-jump} = 26.23 min (SD = 5.76)]. Participants were then asked to complete a series of questionnaires. The Actiheart device was removed, and then the fifth and final saliva sample was provided approximately one-hour post-landing [mean_{post-jump} = 69.79 min (SD = 8.46)].

Before leaving the skydiving facility, participants verbally received instructions for the basal day sample collection in which they were asked to collect their saliva samples on another day at times corresponding with the samples from the skydiving day. Participants were given a basal box kit, including written instructions for saliva collection, and pre-labeled saliva tubes.

On basal days, a researcher contacted every participant using their preferred contact method (phone, text, email) at each sample time as a reminder to provide the sample and to answer any questions regarding the process (Fernandes, Skinner, Woelfel, Carpenter, & Haggerty,

2013). Participants kept the basal day kit in their home freezer immediately after each sample was collected. Once all samples were obtained, the basal box was then returned frozen (using freezer-brix) via courier and then stored at -80°C until assay.

2.3. Measures

2.3.1. Salivary testosterone—On the assay day, saliva samples were thawed and then assayed for testosterone using a commercially available enzyme immunoassay following manufacturer recommendations (www.Salimetrics.com). The intra-assay coefficient of variance (CV) was below 7%, and inter-assay CV was below 15%. All samples were assayed in duplicate. In the case of variance between wells of more than 7%, the assay was re-conducted. Samples from each participant were run on a single microtiter plate to minimize lab-based error variance. All samples were run with antibodies from the same lot. Testosterone values were logarithmically transformed (LnTesto) to normalize the data. These samples were also assayed for cortisol as reported by (Meyer et al., 2015).

2.3.2. Salivary cortisol—We examined cortisol as a moderator of testosterone by calculating a cortisol reactivity score following recommendations Miller et al. (2018). The maximum cortisol score following skydiving was subtracted from the arrival cortisol score so that minimum-maximum change score captured reactivity. We also examined the maximum cortisol score following skydiving as a measure of peak cortisol levels. Given that cortisol reactivity to skydiving from this sample has been previously reported (Meyer et al., 2015), the current manuscript only considers cortisol response with respect to its association with testosterone response.

2.3.3. Autonomic measurements—The Actiheart device (Cambridge Neurotechnology, Ltd.) continuously monitors the QRS complex of the cardiac cycle reliably and validity in non-laboratory settings (Brage, Brage, Franks, Ekelund, & Wareham, 2005), including skydiving (Allison et al., 2012). The Acti-heart processing software automatically discards artifactual measurements when heart rate (HR) is lower than 30, or when an extreme change in HR is recorded including (a) a fluctuation of 100 beats per minute within a one-minute epoch, (b) 120 beats per minute fluctuation within a 30 s epoch, (c) 160 beats per minute fluctuation within a 15 s epoch (CamNtech, 2017). Additionally, data were visually inspected for outliers prior to analysis. HR and HR variability were calculated. HR was defined as number of beats recorded per minute (BPM). Given the reactive nature of the study, a sliding average of HR using 36 s epochs was used. HR variability was measured using the root mean square of successive differences (RMSSD), the successive differences between adjacent or neighboring RR intervals (Berntson, Lozano, & Chen, 2005; Berntson, Quigley, & Lozano, 2007). Like HR, a sliding average of 36 s epochs were calculated for RMSSD.

HR and RMSSD were continuously monitored throughout the skydiving day, but we were specifically interested in whether autonomic reactivity to the jump modulated testosterone reactivity. To extract reactivity scores, we analyzed the individual trends of HR and RMSSD using a time-series model in order (a) to compensate for autocorrelation in time-series data, (b) avoid violating the assumption of independence of observations, (c) minimize the

influence of occasional missing epochs (data were imputed using the *na.kalman* function within *imputeTS* package), and (d) differentiate the influence of subtle variance (i.e. noise) from the underlying time-series trend.

We estimated the time-series model using the *ts* function in R (ver. 3.4.3). We centered each individual's time-series on the time of jump. Although there was variability in the duration of time participants wore the actiheart [mean_{pre-jump} = 25.42 min (SD = 40.85 min), mean_{post-jump} = 18.17 min (SD = 24.37)], a time window of approximately 1 h before the jump to about half an hour after the jump accounted for the majority of the useable data, so we focused analyses within this span of time. Given the extreme nature of the challenge (Goldstein, 2010; Porges, 2009) and our prior work (Allison et al., 2012), we expected that the ANS response to skydiving would span across the duration of the airplane ascent, the jump (5–7 min in free-fall and parachute), and approximately 10 min following the jump before HR or RMSSD reliably declined. In total, this duration amounted to approximately 23 min of an ANS response to skydiving. Separately for HR and RMSSD, we calculated the area under the curve (AUC) score using the *auc* function in R which indexes time-dependent changes in ANS activation across successive epochs, comparable to AUCi (Pruessner, Kirschbaum, Meinlschmid, & Hellhammer, 2003). While this AUC score provides the “area” or amount of autonomic activation during the jump, it does not sufficiently correct for the individual's basal HR or RMSSD level because the extreme nature of the skydiving context makes it unlikely that a participant's basal levels will be achieved in the moments within jumping out of an airplane. Therefore, we calculated a separate AUC score of the total time that participants wore the actiheart device, including the approximately 1 h of time in which they were not actively engaged in skydiving. During this time, participants provided saliva, received instructions, completed questionnaires, and monotonously waited for the airplane to arrive. Prior work suggests little ANS activation during this interval of time (Allison et al., 2012). The following equation was calculated to index the amount of autonomic activation to the jump relative to the overall ANS functioning on the experimental day:

$$\frac{\text{AUC scores after the jump}}{\text{AUC scores on the experimental day}}$$

Separate equations were calculated for HR and RMSSD, respectively, and then standardized for interpretation. Scores beyond 2 SDs from the mean were winsorized (1 participant for HR and 2 participants for RMSSD) to avoid multivariate outliers.

2.3.4. Sensation Seeking—The Sensation Seeking Scale-Version V (SSS-V; Zuckerman, 1979, 1994) measures four domains of SS: thrill and adventure seeking, experience seeking, disinhibition, and boredom susceptibility which can be summed into a total score for sensation seeking traits (Zuckerman, 1979). Reliability estimates for the SSS-V range from .83 to .86 (Zuckerman, 2007).

2.4. Analysis plan

In order to investigate whether the autonomic measures would predict the log-transformed testosterone, we used piecewise growth models analyzed with hierarchical linear modeling

(HLM). The HLM modeled testosterone changes in response to skydiving at Level 1 in order to model time-varying predictors of each sample of testosterone. This approach is similar to our prior work (Phan et al., 2017), and our strategy for modeling cortisol reactivity to skydiving previously with this sample (Meyer et al., 2015). The preliminary model was built:

$$\text{LnTesto}_{ti} =: \beta_{00} + \beta_{10} * \text{TBJ}_{ti} + \beta_{20} * \text{T AJ}_{ti} + \beta_{30} * \text{JB}_{ti} + \beta_{40} * \text{JBXTBJ}_{ti} + \beta_{50} * \text{JBXTAJ}_{ti} + r_{0i} + r_{2i} * \text{TBJ}_{ti} + r_{3i} * \text{T AJ}_{ti} + e_{ti}$$

The Level 1 predictors capture the within-individual time-varying predictors of testosterone levels which then become slopes-as-outcomes in the Level 2 equation. In brief, the intercept (β_{00} *Intercept*) can be interpreted as the individual's basal testosterone levels at the time of the jump because, as described next, other predictor variables were centered on the time of the jump. A predictor for time (in minutes) leading up to the jump captures the slope for testosterone reactivity (β_{10} *Time Before Jump (TBJ)*) and is coded so that higher scores indicate larger or faster reactivity slopes. Time (in minutes) after the jump (β_{30} *Time After Jump (TAJ)*) captures the recovery slope such that higher scores indicate slower drops in testosterone following the jump. This coding for time-varying predictors maps onto the overall pattern of testosterone reactivity and recovery as most participants showed peak levels in testosterone in the sample collected immediately after the jump. Next, the model focused on comparisons between the jump day and time-matched testosterone collected on a basal day. We used a dummy variable (0= basal day; 1= jump day), such that higher scores would describe whether testosterone levels on the jump day were higher than the basal day (β_{30} *Jump* versus *Basal Day (JB)*). There were two terms which captured the change in testosterone on the basal day across the same duration of time (in minutes) as the time-matched samples on the skydiving day leading up to the jump (β_{40} *JB*TBJ*) and then following the jump (β_{50} *JB*TAJ*), respectively; these predictor variables indicate a greater departure of the basal day samples from the jump-day samples.

With this base model established, we then used these Level 1 predictors as outcomes at Level 2 using a slopes-as-outcomes approach. Several potential control variables were examined (e.g., sex, BMI, age, skydiving experience group, oral contraceptives) and, as described below, gender was ultimately included as a control variable in all models. In the model with the full sample size of $N = 44$, we examined whether cortisol reactivity or peak cortisol levels predicted testosterone. We then examined whether the effects of cortisol on testosterone were independent of sensation seeking. Within a subset with autonomic data, we then examined the predictor variables of interest (i.e., HR, RMSSD, SS) using a backwards elimination approach where a predictor was included on all the testosterone components (e.g., level, reactivity, recovery) and then nonsignificant predictors were serially removed until arriving at a parsimonious model where only significant or trend-level predictors of testosterone were modeled. To determine whether autonomic or SS effects on testosterone were overlapping, we then included multiple Level 2 predictors in a single model. Sample size limitations precluded the possibility of examining whether autonomic, SS and cortisol independently impacted testosterone.

3. Results

HLM analyses were conducted to measure change in T concentrations in response to skydiving. An intraclass correlation analysis indicated that 84% of the variance in T concentrations was accounted for by between-subjects differences [ICC = .84, $p < .0001$], whereas sample-to-sample fluctuations in testosterone accounted for 16% of variance T levels. Descriptive statistics for the sample are provided in Table 1. No significant correlations between covariates of interest (SS, parasympathetic activation, sympathetic activation) were observed (see Table 2).

We hypothesized that testosterone would be reactive to skydiving. We found that participants showed a significant rise in T levels leading up to the jump [$\beta = 0.199$, $t_{(43)} = 5.68$, $p < 0.001$], followed by a decline in T following the jump [$\beta = -0.201$, $t_{(43)} = -4.04$, $p < 0.001$], hereafter termed reactivity and recovery, respectively (Fig. 1). Moreover, peak T levels were significantly higher on the jump day relative to the time-matched basal day [$\beta = 0.269$, $t_{(43)} = 2.25$, $p = 0.030$]. Fixed predictors for T reactivity and recovery changes on the basal day showed that, compared to the jump day, the reactivity interval on the basal day showed a significantly smaller (if any) rise [$\beta = -.201$, $t(129) = -3.47$, $p = .002$] and the recovery interval showed a significantly less steep recovery decline [$\beta = .246$, $t(129) = 3.08$, $p = .003$] as compared to the equivalent interval of time on the skydiving day.

Next, we examined the moderating effects of gender and other potential control variables on T levels and T response to skydiving. When added to the model, gender was a significant predictor of overall T levels [$\beta = -1.312$, $t_{(42)} = -5.41$, $p < 0.001$] such that males had higher T than females. However, gender did not significantly predict changes in T reactivity [$\beta = -0.004$, $t = -0.060$, $p = 0.953$] or recovery [$\beta = 0.110$, $t = 1.18$, $p = 0.246$] to skydiving. Participant age did not predict testosterone levels, reactivity or recovery, $ps > .23$. BMI did not predict testosterone levels, reactivity or recovery, $ps > .29$. Group (novice vs experienced jumpers) did not influence testosterone levels [$\beta = 0.38$, $t(41) = 1.23$, $p = 0.22$], reactivity [$\beta = -.166$, $t(42) = -1.44$, $p = 0.159$], or recovery, [$\beta = 0.07$, $t(42) = 0.35$, $p = 0.73$], although there was a trend for experienced skydivers to have a smaller difference between jump and basal days compared to novice jumpers [$\beta = -.577$, $t(169) = -1.69$, $p = 0.093$]. As such, gender was included as a covariate for testosterone levels (i.e., the intercept) in all subsequent models. Female participants' use of oral contraceptives was noted; however, contraception use did not alter any of the findings presented.

To test the hypothesis that increased T levels would be associated with increased sensation seeking scores, SS was entered as a predictor of testosterone responsiveness to skydiving. Higher SS was associated with greater T reactivity [$\beta = 0.009$, $t_{(34)} = 2.48$, $p = 0.018$] (Fig. 2).

Cortisol reactivity's impact on testosterone reactivity to skydiving was investigated next. Greater cortisol reactivity to skydiving was associated with greater testosterone reactivity to skydiving [$\beta = .056$, $t_{(42)} = 2.57$, $p = 0.011$] (Fig. 3). We also found that individuals with higher peak cortisol levels also had higher testosterone levels [$\beta = .431$, $t_{(41)} = -3.91$, $p < 0.001$]. Critically, both SS and cortisol reactivity persisted as significant predictors of

testosterone reactivity when simultaneously modeled, such that individuals with higher SS [$\beta=.014$, $t_{(41)}=2.92$, $p<0.006$] or higher cortisol reactivity [$\beta=.061$, $t_{(41)}=2.64$, $p<0.012$] showed greater testosterone reactivity (Table 3). Similarly when examining peak cortisol levels and SS simultaneously, peak cortisol levels continued to predict testosterone levels [$\beta=.428$, $t_{(40)}=-3.89$, $p<0.001$] and SS continued to predict testosterone reactivity [$\beta=.014$, $t_{(42)}=2.38$, $p<0.022$] (see Table 3).

A total of 36 subjects had valid hormone and autonomic data, so all further analyses were conducted within this subsample. We first tested whether HR modulate T levels and responsivity to skydiving. Higher HR responses during skydiving was associated with faster T reactivity [$\beta=0.073$, $t_{(34)}=2.73$, $p=0.010$] and faster recovery [$\beta=-0.102$, $t_{(34)}=-2.48$, $p=0.020$] (Fig. 2). Next, RMSSD responsivity to skydiving was considered. Individuals with higher RMSSD showed lower levels of T overall [$\beta=-0.335$, $t_{(34)}=-2.67$, $p=0.012$] and less T reactivity [$\beta=-0.106$, $t_{(34)}=-3.48$, $p=0.001$] (Fig. 2). Individuals with greater elevations in RMSSD during skydiving also showed a greater difference in T on the jump relative to the basal day [$\beta=0.294$, $t_{(34)}=2.57$, $p=0.015$]. Fig. 2 shows that individuals with low RMSSD had elevated testosterone levels across both basal and jump days, but individuals with high RMSSD had low testosterone levels on the basal day and only displayed high testosterone levels on the jump day. Given that HR is influenced by both sympathetic and parasympathetic branches whereas RMSSD is largely under parasympathetic control, we attempted to differentiate the two autonomic branches by including both HR and RMSSD in the same model (Allison et al., 2012). Table 3 shows that effects of HR on T reactivity and recovery persisted after controlling for RMSSD and, similarly, effects of RMSSD on T levels, basal day levels, and reactivity persisted suggesting that sympathetic and parasympathetic influences on T are distinct.

We confirmed within this subset that SS scores persisted as a predictor of testosterone responsiveness to skydiving. Higher SS was associated with greater T reactivity [$\beta=0.009$, $t_{(34)}=2.48$, $p=0.018$] and a faster T recovery [$\beta=-0.014$, $t_{(42)}=-2.67$, $p=0.012$]. Furthermore, Table 4 shows that effects of SS on T reactivity and recovery persisted after controlling for HR or RMSSD, respectively. Finally, a model was run, including HR AUC, RMSSD and SS as predictors of T at the levels where they were significant predictors in the above analyses (see Table 4). The results of this model were consistent with the original findings, though some relationships dropped to trend levels.

4. Discussion

The current study examined the relationship between SS and testosterone reactivity and the degree to which that relationship is modulated by stress responsivity, including cortisol and ANS reactivity. There were five main findings. First, testosterone reactivity and recovery were observed during skydiving. Furthermore, males showed greater levels of testosterone, but no significant gender differences in the pattern of reactivity nor recovery were observed. Second, individuals with higher levels of SS had faster testosterone reactivity and faster T recovery. Third, greater cortisol reactivity and higher peak cortisol levels were associated with higher testosterone reactivity and testosterone levels, respectively. Critically, SS remained a predictor of testosterone reactivity even when cortisol was entered into the

model. Fourth, higher levels of testosterone were related to ANS functioning. Specifically, as indicated by HR, increased sympathetic response to skydiving was related to greater testosterone reactivity and a faster recovery. Conversely, as indicated by RMSSD, increased parasympathetic response to skydiving was associated with reduced overall levels of testosterone and reduced testosterone recovery after jumping. Finally, in an exploratory analysis, the patterns of these relationships remained when sympathetic, parasympathetic, and SS were all included in the same model, suggesting effects are distinct.

4.1. Skydiving and testosterone response

Consistent with hypotheses, testosterone was reactive to skydiving, such that testosterone secretion increased leading up to the jump and then declined, or recovered, after the jump. These changes were not observed on a time-matched basal day where testosterone levels remained relatively flat across the same duration of time. Testosterone reactivity is consistent with the common conceptualization of skydiving as an SS activity, as well as with other psychobiological work (e.g., Allison et al., 2012). Moreover, individuals with higher levels of SS had faster testosterone reactivity and faster T recovery, further linking SS and testosterone response.

The current findings, however, stand in contrast to previous work that found *reduced* testosterone on a jump day relative to a basal day (Chatterton et al., 1997). However, testosterone has a diurnal rhythm and it is expected that testosterone will decrease over the course of the day (e.g., Khan-Dawood et al., 1984; Plymate et al., 1989). Chatterton et al. (1997) obtained their measures of testosterone in the morning and then the skydive took place in early afternoon. Thus, the timing of the testosterone samples leaves open the possibility that the decrease observed was, all or in part, due to normal circadian variations in testosterone. Furthermore, the data from that earlier study appeared to show a rise in testosterone immediately following the jump, though this change was not significant (Chatterton et al., 1997; see Figure 7). Thus, Chatterton et al. (1997) observed a non-significant rise in testosterone in response to skydiving in the context of decreasing testosterone levels across the day consistent with the diurnal rhythm. Moreover, Chatterton and colleagues did not assess the degree to which participants enjoyed the experience of skydiving. Thus, a subset of participants in that study may have responded to the task as a negative stressor rather than a thrilling or exciting experience. In contrast, participants in the current study endorsed sustained high levels of happiness following skydiving, suggesting that this activity was pleasurable for this group individuals (Meyer et al., 2015). These findings are consistent with the idea that individual differences when examining neuroendocrine responses as the same context can exert a very different physiological impact from one individual to another (e.g., Josephs, Mehta, & Carré, 2011).

4.2. Cortisol, and testosterone response to skydiving

Previous work with this sample reported an increase in cortisol following skydiving (Meyer et al., 2015). The present study builds upon this observation to reveal that cortisol reactivity and peak levels were positively associated with testosterone reactivity and levels, respectively. The dual-axis hypothesis (Pranjal H. Mehta & Josephs, 2010) and the view that situations viewed as threatening or stressful engender an cortisol response, while challenging

situations stimulate a testosterone response (Wobber et al., 2010) lent to the prediction for a negative relationship between testosterone and cortisol reactivity to skydiving. Support for this theory was not apparent as we revealed positive HPA- HPG associations, and we revealed that the relationship between SS and testosterone reactivity remained significant even with cortisol in the model. Instead, our findings support a “coupling” model where the HPA and HPG axis positively modulate one another, and extends the subset of that literature that examines acute reactivity (Marceau et al., 2014; Phan et al., 2017; Zakreski et al., 2019) to skydiving. This suggests situations that are both stressful and exciting, like skydiving, may simultaneously activate both the HPA and HPG axes, possibly helping the individual to navigate a situation which is thrilling precisely because it is both stressful and challenging.

4.3. ANS modulation of testosterone response to skydiving

Also consistent with hypotheses, the present study found that sympathetic nervous system stress biomarkers, as indicated by HR, modulated testosterone reactivity. Participants who showed higher HR levels at the time of jump showed faster T reactivity and faster T recovery following the jump. Moreover, the HR response persisted even when controlling for parasympathetic activation (as indicated by RMSSD) suggesting that sympathetic activation was driving the HR response. Sympathetic response serves to increase somatic arousal, which is typically described as the “fight or flight” response (Kemeny, 2003), although in positively valenced situations might also be described as the “excite and delight” response (Allison et al., 2012). It is possible that both T and sympathetic response work together in exciting contexts to enhance the positive valence of a context over time. Certainly, there is substantial evidence to suggest that there is a complex interplay between the brain and both neuroendocrine systems (including testosterone) and the ANS (Hastings & Miller, 2014; Kreibig, 2010; Thayer, Ahs, Fredrikson, Sollers, & Wager, 2012). Indeed, it has been proposed that pre-genual anterior cingulate cortex/rostral-medial prefrontal cortex plays a critical role in the modulation of both the ANS and neuroendocrine systems (Thayer et al., 2012).

T levels and reactivity were also related to parasympathetic functioning, as indicated by RMSSD wherein higher RMSSD scores indicate a greater propensity for the individual to be able to “rest and digest” or remain physiologically calm (S. W. Porges, 2007). Individuals showing high levels of RMSSD during the jump showed equivalently high levels of T on jump day relative to individuals with low levels of RMSSD. On the basal day, however, individuals who had been able to maintain high levels of RMSSD and remain physiologically calm despite jumping out of an airplane, had lower levels of basal T on a non-challenge day (see Fig. 1). Moreover, and consistent with previous findings that individuals with high resting parasympathetic tone had reduced testosterone reactivity (E. C. Porges et al., 2015), increased RMSSD was also associated with lower T reactivity to skydiving. In other words, higher levels of tonic parasympathetic activation were associated with reduced levels of T in the absence of a major SS event like skydiving and reduced reactivity *to* a major SS event. The parasympathetic nervous system plays a crucial role in maintaining homeostasis under basal or tonic states (Beauchaine, 2001; S. W. Porges, 2007), helping to keep activity of the sympathetic nervous system in check or, within stress states, reducing its tonic control over the autonomic nervous system to allow for efficient activation

of the stress system (Porges, 1995). The present study suggests that the regulatory role of the parasympathetic nervous system may be broad, extending to a role in regulating T levels and responsivity. However, the current data cannot speak to any potential mechanism and future work will need to examine this possibility.

4.4. Sensation seeking, stress biomarkers and testosterone

As previously reported (Allison et al., 2012; Meyer et al., 2015), participants in the current study reported positive emotions and showed ANS activation consistent with experiencing an enjoyable rush during skydiving. The current data also show that this pleasurable activity was associated with increased testosterone reactivity consistent with suggestions that testosterone release is pleasurable (Chichinadze, Lazarashvili, Chichinadze, & Gachechiladze, 2012) and observations of testosterone increases in contexts that are exciting (e.g., sex; Escasa, Casey, & Gray, 2011; Hirschenhauser, Frigerio, Grammer, & Magnusson, 2002). Physical, visceral sensations play an important role in decision-making (Paulus, 2007). It is plausible that positive physical sensations during risk-taking increase the value of exciting/risky behaviors in those endorsing increased levels of SS, making exciting/risky behaviors more likely.

Notably, however, results suggest that the impact of stress biomarkers and SS were independently related to testosterone response. Indeed, not only did the associations of HR, RMSSD, and SS showed independent effects on T but, in addition, HR, RMSSD and SS were not significantly correlated in the current study (Table 2). The subjective experience of emotions is shaped by appraisal of the context (Lazarus, 2006). However, while there was undoubtedly physiological activation of testosterone during skydiving and further modulation of testosterone reactivity by both autonomic branches, as well as cortisol, these physiological effects did not necessarily translate into SS traits. This suggests a more complex origin of SS than physiological response during the experience of an intense context.

These findings therefore have potential clinical relevance. Reducing the “rush” sensation associated with risk taking might represent a useful treatment goal in individuals exhibiting maladaptive behaviors associated with increased SS, including substance-abuse (Stautz & Cooper, 2013), risky-sexual behavior (Charnigo et al., 2013) and antisocial behavior (Mann et al., 2017; Wilson & Scarpa, 2014). By reducing the positive physical sensations associated with exciting/risky behaviors, a positive reinforcer would be removed, making the behaviors less likely in the future. However, the current data suggest that a more comprehensive understanding of psychobiology of SS will be needed to establish treatment targets.

4.5. Testosterone response and gender

Much like the extant literature on the topic of gender differences, hypotheses with respect to gender were not entirely supported and primarily showed subtle differences between males and females (Zahn-Waxler, Shirtcliff, & Marceau, 2008). Although there was the expected gender difference in testosterone levels, the data did not support the hypothesis that there would be additional difference in testosterone reactivity in males and females. There are at

least three possible interpretations of these data. First, it is possible that testosterone reactivity does not differ between men and women. Crewther et al. (2016), examining Olympic weight-lifters, and Jiménez et al. (2012), examining community badminton players, also found no gender differences in testosterone reactivity to competition. Second, it is possible that testosterone reactivity *does* differ between men and women, but differences may be obscured by sampling factors. For example, the current study was likely under-powered to examine sex differences. Moreover, skydiving is a predominantly male sport (Westman & Bjornstig, 2007) and women who choose to skydive may represent a unique female population. A random sampling of males and females might yield significant gender differences. Third, testosterone reactivity may play a similar role in both males and females, but context, including experimental design, may largely determine whether testosterone reactivity will or will not manifest gender differences. For example, when male and female athletes are compared when competing, no differences have been observed (Crewther et al., 2016; Jiménez et al., 2012). However, during within team practice competitions (Kivlighan et al., 2005), video game competitions (Carré et al., 2013; Mazur, Susman, & Edelbrock, 1997), and response to election results (Stanton, Beehner, Saini, Kuhn, & Labar, 2009), gender differences in testosterone reactivity have been observed. It is possible that these contexts have a different meaning for men and women and that it is these differences in contextual factors that is driving differences in testosterone reactivity, as opposed to physiological gender differences. Future work will need to examine this possibility.

4.6. Limitations

The current data should be interpreted in the light of three caveats. First, the sample size, while relatively typical for the field, was modest. Replication in larger samples, particularly with respect to the gender-based analyses, is needed. Second, the sample included both experienced and novice sky-divers. While experience did not appear to impact testosterone levels, reactivity or recovery, experience plays a role in cortisol reactivity (Meyer et al., 2015). The current study may have been under-powered to detect this difference for testosterone. Finally, there has been some suggestion in the literature that enzyme-linked immunoassay techniques, like the ones used in the current study, may under-estimate testosterone levels in women (see, for example, Welker et al., 2016). It is possible that an alternate method of assaying testosterone might have uncovered significant gender differences in reactivity, though it should be noted that in the current study testosterone reactivity was observed in both males and females equally.

4.7. Conclusion

Sensation-seeking is a risk-factor for important negative outcomes, including substance-abuse (Stautz & Cooper, 2013), risky-sexual behavior (Charnigo et al., 2013) and antisocial behavior (Mann et al., 2017; Wilson & Scarpa, 2014). The current data suggest that testosterone reactivity, and its relationship to ANS responsivity, may play a role in providing individuals with a pleasurable response to risky and/or intense situations. Moving beyond a single biomarker, the data suggest that multiple physiological systems may instantiate the “excite and delight” of skydiving within motivated and willing volunteers, and, furthermore, these systems may work together to instantiate, maintain and sustain such a physiological

and behavioral response. Moving beyond skydiving, these data may prove useful in developing novel intervention strategies for antisocial behavior, including substance abuse.

Acknowledgements

This work was supported by the National Institute of Mental Health, National Institutes of Health in grants to Dr. White (K01-MH110643) and Dr. Shirtcliff (K01-MH077687). The authors wish to thank Jeremy Peres, Justin Vaughn, Melissa Warner, Amber Allison, Christian Boettger, Uwe Leonbacher, Vanessa Meyer, Swornim Shrestha, Amanda Piglia, Brittany Verret, Gold Coast Skydivers and the study participants.

References

- Allison AL, Peres JC, Boettger C, Leonbacher U, Hastings PD, & Shirtcliff EA (2012). Fight, flight, or fall: Autonomic nervous system reactivity during skydiving. *Personality and Individual Differences*, 53(3), 218–223. 10.1016/j.paid.2012.03.019.
- Apicella CL, Dreber A, & Mollerstrom J (2014). Salivary testosterone change following monetary wins and losses predicts future financial risk-taking. *Psychoneuroendocrinology*, 39, 58–64. 10.1016/j.psyneuen.2013.09.025. [PubMed: 24275004]
- Archer J (2006). Testosterone and human aggression: An evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, 30(3), 319–345. 10.1016/j.neubiorev.2004.12.007. [PubMed: 16483890]
- Arnold AP, & Breedlove SM (1985). Organizational and activational effects of sex steroids on brain and behavior: A reanalysis. *Hormones and Behavior*, 19(4), 469–498. [PubMed: 3910535]
- Bateup HS, Booth A, Shirtcliff EA, & Granger DA (2002). Testosterone, cortisol, and women's competition. *Evolution and Human Behavior*, 23(3), 181–192. 10.1016/S1090-5138(01)00100-3.
- Beauchaine T (2001). Vagal tone, development, and Gray's motivational theory: Toward an integrated model of autonomic nervous system functioning in psychopathology. *Development and Psychopathology*, 13(2), 183–214. [PubMed: 11393643]
- Berntson GG, Lozano DL, & Chen Y-J (2005). Filter properties of root mean square successive difference (RMSSD) for heart rate. *Psychophysiology*, 42(2), 246–252. 10.1111/j.1469-8986.2005.00277.x. [PubMed: 15787862]
- Berntson GG, Quigley KS, & Lozano D (2007). Cardiovascular psychophysiology The handbook of psychophysiology (third edition). Cambridge, England: Cambridge University Press 182–210.
- Booth A, Shelley G, Mazur A, Tharp G, & Kittok R (1989). Testosterone, and winning and losing in human competition. *Hormones and Behavior*, 23(4), 556–571. [PubMed: 2606468]
- Brage S, Brage N, Franks PW, Ekelund U, & Wareham NJ (2005). Reliability and validity of the combined heart rate and movement sensor Actiheart. *European Journal of Clinical Nutrition*, 59(4), 561–570. 10.1038/sj.ejcn.1602118. [PubMed: 15714212]
- CamNtech (2017). ActiHeart user manual (4.0.129). Cambridge, England: CamNtech, Inc.
- Campbell BC, Dreber A, Apicella CL, Eisenberg DTA, Gray PB, Little AC, ... Lum JK (2010). Testosterone exposure, dopaminergic reward, and sensation seeking in young men. *Physiology & Behavior*, 99(4), 451–456. 10.1016/j.physbeh.2009.12.011. [PubMed: 20026092]
- Carré JM, & Mehta PH (2011). Importance of considering testosterone-cortisol interactions in predicting human aggression and dominance. *Aggressive Behavior*, 37(6), 489–491. 10.1002/ab.20407. [PubMed: 21826676]
- Carré JM, Campbell JA, Lozoya E, Goetz SMM, & Welker KM (2013). Changes in testosterone mediate the effect of winning on subsequent aggressive behaviour. *Psychoneuroendocrinology*, 38(10), 2034–2041. 10.1016/j.psyneuen.2013.03.008. [PubMed: 23587440]
- Casto KV, Rivell A, & Edwards DA (2017). Competition-related testosterone, cortisol, and perceived personal success in recreational women athletes. *Hormones and Behavior*, 92, 29–36. <https://doi.org/10.1016/j.yhbeh.2017.05.006>. [PubMed: 28527589]
- Charnigo R, Noar SM, Garnett C, Crosby R, Palmgreen P, & Zimmerman RS (2013). Sensation seeking and impulsivity: Combined associations with risky sexual behavior in a large sample of

- young adults. *Journal of Sex Research*, 50(5), 480–488. 10.1080/00224499.2011.652264. [PubMed: 22456443]
- Chatterton RT, Vogelsong KM, Lu YC, & Hudgens GA (1997). Hormonal responses to psychological stress in men preparing for skydiving. *The Journal of Clinical Endocrinology and Metabolism*, 82(8), 2503–2509. 10.1210/jcem.82.8.4133. [PubMed: 9253325]
- Chichinadze K, Lazarashvili A, Chichinadze N, & Gachechiladze L (2012). Testosterone dynamics during encounter: Role of emotional factors. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 198(7), 485–494. 10.1007/s00359-012-0726-1.
- Coates JM, & Herbert J (2008). Endogenous steroids and financial risk taking on a London trading floor. *Proceedings of the National Academy of Sciences of the United States of America*, 105(16), 6167–6172. 10.1073/pnas.0704025105. [PubMed: 18413617]
- Crewther B, Obminski Z, & Cook C (2016). The effect of steroid hormones on the physical performance of boys and girls during an olympic weightlifting competition. *Pediatric Exercise Science*, 28(4), 580–587. 10.1123/pes.2016-0070. [PubMed: 27615264]
- Do ru MT, Ba ar MM, Yuvaç E, Sim ek V, & Sahin O (2010). The relationship between serum sex steroid levels and heart rate variability parameters in males and the effect of age. *Türk Kardiyoloji Demegi Arsivi: Turk Kardiyoloji Demeginin Yayin Organidir*, 38(7), 459–465.
- Edwards DA, & Casto KV (2013). Women's intercollegiate athletic competition: Cortisol, testosterone, and the dual-hormone hypothesis as it relates to status among teammates. *Hormones and Behavior*, 64(1), 153–160. 10.1016/j.yhbeh.2013.03.003. [PubMed: 23523743]
- Ermiş N, Deniz F, Kepez A, Kara B, Azal O, & Kutlu M (2010). Heart rate variability of young men with idiopathic hypogonadotropic hypogonadism. *Autonomic Neuroscience: Basic & Clinical*, 152(1–2), 84–87. <https://doi.org/10.1016/Zj.autneu.2009.08.018>. [PubMed: 19766543]
- Escasa MJ, Casey JF, & Gray PB (2011). Salivary testosterone levels in men at a U.S. Sex club. *Archives of Sexual Behavior*, 40(5), 921–926. 10.1007/s10508-010-9711-3. [PubMed: 21165688]
- Fernandes A, Skinner ML, Woelfel T, Carpenter T, & Haggerty KP (2013). Implementing self-collection of biological specimens with a diverse sample. *Field Methods*, 25(1), 10.1177/1525822X12453526.
- Freixanet MGI (1999). Personality profile of subjects engaged in high physical risk sports. *Human Performance in Extreme Environments : the Journal of the Society for Human Performance in Extreme Environments*, 4(2), 11–17.
- Geniole SN, Busseri MA, & McCormick CM (2013). Testosterone dynamics and psychopathic personality traits independently predict antagonistic behavior towards the perceived loser of a competitive interaction. *Hormones and Behavior*, 64(5), 790–798. 10.1016/j.yhbeh.2013.09.005. [PubMed: 24120551]
- Goldstein DS (2010). Adrenal responses to stress. *Cellular and Molecular Neurobiology*, 30(8), 1433–1440. 10.1007/s10571-010-9606-9. [PubMed: 21061156]
- Granger DA, Shirtcliff EA, Booth A, Kivlighan KT, & Schwartz EB (2004). The “trouble” with salivary testosterone. *Psychoneuroendocrinology*, 29(10), 1229–1240. 10.1016/j.psyneuen.2004.02.005. [PubMed: 15288702]
- Granger DA, Shirtcliff EA, Zahn-Waxler C, Usher B, Klimes-Dougan B, & Hastings P (2003). Salivary testosterone diurnal variation and psychopathology in adolescent males and females: Individual differences and developmental effects. *Development and Psychopathology*, 15(2), 431–449. [PubMed: 12931836]
- Green M, Turner C, Purdie DM, & McClure R (2003). Injury related risk behavior-a study of Australian skydivers. *Journal of Science and Medicine in Sport*, 6(2), 166–175. [PubMed: 12945623]
- Hare OA, Wetherell MA, & Smith MA (2013). State anxiety and cortisol reactivity to skydiving in novice versus experienced skydivers. *Physiology & Behavior*, 118, 40–44. 10.1016/j.physbeh.2013.05.011. [PubMed: 23685228]
- Hart CL, Griffith JD, & Randell JA (2006). An analysis of U.S. Parachuting fatalities: 2000–2004. *Perceptual and Motor Skills*, 103(3), 896–900. 10.2466/pms.103.3.896-900. [PubMed: 17326520]

- Hasegawa M, Toda M, & Morimoto K (2008). Changes in salivary physiological stress markers associated with winning and losing. *Biomedical Research (Tokyo, Japan)*, 29(1), 43–46.
- Hastings PD, & Miller JG (2014). *Autonomic regulation, polyvagal theory, and children's prosocial development*. Prosocial development: A multidimensional approach. New York, NY, US: Oxford University Press 112–127. 10.1093/acprof:oso/9780199964772.003.0006.
- Hirschenhauser K, Frigerio D, Grammer K, & Magnusson MS (2002). Monthly patterns of testosterone and behavior in prospective fathers. *Hormones and Behavior*, 42(2), 172–181. [PubMed: 12367570]
- Jiménez M, Aguilar R, & Alvero-Cruz JR (2012). Effects of victory and defeat on testosterone and cortisol response to competition: Evidence for same response patterns in men and women. *Psychoneuroendocrinology*, 37(9), 1577–1581. 10.1016/j.psyneuen.2012.02.011. [PubMed: 22429747]
- Josephs RA, Mehta PH, & Carré JM (2011). Gender and social environment modulate the effects of testosterone on social behavior: Comment on Eisenegger et al. *Trends in Cognitive Sciences*, 15(11), 509–510. [PubMed: 21974876]
- Kandeel FR, Koussa VK, & Swerdloff RS (2001). Male sexual function and its disorders: Physiology, pathophysiology, clinical investigation, and treatment. *Endocrine Reviews*, 22(3), 342–388. 10.1210/edrv.22.3.0430. [PubMed: 11399748]
- Kemeny ME (2003). The psychobiology of stress. *Current Directions in Psychological Science*, 12(4), 124–129. 10.1111/1467-8721.01246.
- Khan-Dawood FS, Choe JK, & Dawood MY (1984). Salivary and plasma bound and “free” testosterone in men and women. *American Journal of Obstetrics and Gynecology*, 148(4), 441–445. [PubMed: 6538069]
- Kivlighan KT, Granger DA, & Booth A (2005). Gender differences in testosterone and cortisol response to competition. *Psychoneuroendocrinology*, 30(1), 58–71. 10.1016/j.psyneuen.2004.05.009. [PubMed: 15358443]
- Kreibig SD (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, 84(3), 394–421. 10.1016/j.biopsycho.2010.03.010. [PubMed: 20371374]
- Lazarus RS (2006). Emotions and interpersonal relationships: Toward a person-centered conceptualization of emotions and coping. *Journal of Personality*, 74(1), 9–46. 10.1111/j.1467-6494.2005.00368.x. [PubMed: 16451225]
- Mann FD, Engelhardt L, Briley DA, Grotzinger AD, Patterson MW, Tackett JL, ... Harden KP (2017). Sensation seeking and impulsive traits as personality endophenotypes for antisocial behavior: Evidence from two independent samples. *Personality and Individual Differences*, 105, 30–39. . [PubMed: 28824215]
- Marceau K, Ruttle PL, Shirtcliff EA, Essex MJ, & Susman EJ (2015). Developmental and contextual considerations for adrenal and gonadal hormone functioning during adolescence: Implications for adolescent mental health. *Developmental Psychobiology*, 57(6), 742–768. 10.1002/dev.21214. [PubMed: 24729154]
- Marceau K, Shirtcliff EA, Hastings PD, Klimes-Dougan B, Zahn-Waxler C, Dorn LD, ... Susman EJ (2014). Within-adolescent coupled changes in cortisol with DHEA and testosterone in response to three stressors during adolescence. *Psychoneuroendocrinology*, 41, 33–45. . [PubMed: 24495606]
- Mazur A, Susman EJ, & Edelbrock S (1997). Sex difference in testosterone response to a video game contest. *Evolution and Human Behavior*, 18(5), 317–326. 10.1016/S1090-5138(97)00013-5.
- Mehta PH, & Josephs RA (2010). Testosterone and cortisol jointly regulate dominance: Evidence for a dual-hormone hypothesis. *Hormones and Behavior*, 58(5), 898–906. <https://doi.org/10.1016/j.yhbeh.2010.08.020>. [PubMed: 20816841]
- Mehta PH, Jones AC, & Josephs RA (2008). The social endocrinology of dominance: Basal testosterone predicts cortisol changes and behavior following victory and defeat. *Journal of Personality and Social Psychology*, 94(6), 1078–1093. 10.1037/0022-3514.94.6.1078. [PubMed: 18505319]
- Mehta PH, Welker KM, Zilioli S, & Carré JM (2015). Testosterone and cortisol jointly modulate risk-taking. *Psychoneuroendocrinology*, 56, 88–99. 10.1016/j.psyneuen.2015.02.023. [PubMed: 25813123]

- Meyer VJ, Lee Y, Böttger C, Leonbacher U, Allison AL, & Shirtcliff EA (2015). Experience, cortisol reactivity, and the coordination of emotional responses to skydiving. *Frontiers in Human Neuroscience*, 9, 138. [PubMed: 25859199]
- Miller R, Wojtyniak J-G, Weckesser LJ, Alexander NC, Engert V, & Lehr T (2018). How to disentangle psychobiological stress reactivity and recovery: A comparison of model-based and non-compartmental analyses of cortisol concentrations. *Psychoneuroendocrinology*, 90, 194–210. 10.1016/j.psyneuen.2017.12.019. [PubMed: 29370954]
- Musolino RF, & Hershenson DB (1977). Avocational sensation seeking in high and low risk-taking occupations. *Journal of Vocational Behavior*, 10(3), 358–365. 10.1016/0001-8791(77)90069-0..
- Oliveira T, Gouveia MJ, & Oliveira RF (2009). Testosterone responsiveness to winning and losing experiences in female soccer players. *Psychoneuroendocrinology*, 34(7), 1056–1064. 10.1016/j.psyneuen.2009.02.006. [PubMed: 19278791]
- Paulus MP (2007). Decision-making dysfunctions in psychiatry-altered homeostatic processing? *Science (New York, NY)*, 318(5850), 602–606.
- Perini T, Ditzen B, Hengartner M, & Ehler U (2012). Sensation seeking in fathers: The impact on testosterone and paternal investment. *Hormones and Behavior*, 61 (2), 191–195. 10.1016/j.yhbeh.2011.12.004. [PubMed: 22198307]
- Phan JM, Schneider E, Peres J, Miocevic O, Meyer V, & Shirtcliff EA (2017). Social evaluative threat with verbal performance feedback alters neuroendocrine response to stress. *Hormones and Behavior*, 96, 104–115. 10.1016/j.yhbeh.2017.09.007. [PubMed: 28919553]
- Plymate SR, Tenover JS, & Bremner WJ (1989). Circadian variation in testosterone, sex hormone-binding globulin, and calculated non-sex hormone-binding globulin bound testosterone in healthy young and elderly men. *Journal of Andrology*, 10(5), 366–371. [PubMed: 2592266]
- Porges SW (1995). Cardiac vagal tone: A physiological index of stress. *Neuroscience and Biobehavioral Reviews*, 19(2), 225–233. [PubMed: 7630578]
- Porges SW (2007). The polyvagal perspective. *Biological Psychology*, 74(2), 116–143. 10.1016/j.biopsycho.2006.06.009. [PubMed: 17049418]
- Porges SW (2009). The polyvagal theory: New insights into adaptive reactions of the autonomic nervous system. *Cleveland Clinic Journal of Medicine*, 76(Suppl. 2), S86–90. 10.3949/ccjm.76.s2.17. [PubMed: 19376991]
- Porges EC, Smith KE, & Decety J (2015). Individual differences in vagal regulation are related to testosterone responses to observed violence. *Frontiers in Psychology*, 6, 19 10.3389/fpsyg.2015.00019. [PubMed: 25759673]
- Pruessner JC, Kirschbaum C, Meinlschmid G, & Hellhammer DH (2003). Two formulas for computation of the area under the curve represent measures of total hormone concentration versus time-dependent change. *Psychoneuroendocrinology*, 28(7), 916–931. [PubMed: 12892658]
- Radtke T, Poerschke D, Wilhelm M, Trachsel LD, Tschanz H, Matter F, ... Schmid J-P (2016). Acute effects of Finnish sauna and cold-water immersion on haemodynamic variables and autonomic nervous system activity in patients with heart failure. *European Journal of Preventive Cardiology*, 23(6), 593–601. 10.1177/2047487315594506. [PubMed: 26152773]
- Richter SD, Schurmeyer TH, Schedlowski M, Hadicke A, Tewes U, Schmidt RE, ... Wagner TO (1996). Time kinetics of the endocrine response to acute psychological stress. *The Journal of Clinical Endocrinology and Metabolism*, 81(5), 1956–1960. 10.1210/jcem.81.5.8626864. [PubMed: 8626864]
- Schultheiss OC, Wirth MM, & Stanton SJ (2004). Effects of affiliation and power motivation arousal on salivary progesterone and testosterone. *Hormones and Behavior*, 46(5), 592–599. <https://doi.org/10.1016/j.yhbeh.2004.07.005>. [PubMed: 15555501]
- Shirtcliff EA, Dahl RE, & Pollak SD (2009). Pubertal development: Correspondence between hormonal and physical development. *Child Development*, 80(2), 327–337. 10.1111/j.1467-8624.2009.01263.x. [PubMed: 19466995]
- Shirtcliff EA, Dismukes AR, Marceau K, Ruttle PL, Simmons JG, & Han G (2015). A dual-axis approach to understanding neuroendocrine development. *Developmental Psychobiology*, 57(6), 643–653. 10.1002/dev.21337. [PubMed: 26220016]

- Shirtcliff EA, Granger DA, & Likos A (2002). Gender differences in the validity of testosterone measured in saliva by immunoassay. *Hormones and Behavior*, 42(1), 62–69. [PubMed: 12191648]
- Stanton SJ, Beehner JC, Saini EK, Kuhn CM, & Labar KS (2009). Dominance, politics, and physiology: Voters' testosterone changes on the night of the 2008 United States presidential election. *PloS One*, 4(10), e7543 [PubMed: 19844583]
- Stautz K, & Cooper A (2013). Impulsivity-related personality traits and adolescent alcohol use: A meta-analytic review. *Clinical Psychology Review*, 33(4), 574–592. 10.1016/j.cpr.2013.03.003. [PubMed: 23563081]
- Thayer JF, Ahs F, Fredrikson M, Sollers JJ, & Wager TD (2012). A meta-analysis of heart rate variability and neuroimaging studies: Implications for heart rate variability as a marker of stress and health. *Neuroscience and Biobehavioral Reviews*, 36(2), 747–756. 10.1016/j.neubiorev.2011.11.009. [PubMed: 22178086]
- Thronquist MH, Zuckerman M, & Exline RV (1991). Loving, liking, looking and sensation seeking in unmarried college couples. *Personality and Individual Differences*, 12(12), 1283–1292. 10.1016/0191-8869(91)90202-M.
- Viau V (2002). Functional cross-talk between the hypothalamic-pituitary-gonadal and -adrenal axes. *Journal of Neuroendocrinology*, 14(6), 506–513. [PubMed: 12047726]
- Welker KM, Lassetter B, Brandes CM, Prasad S, Koop DR, & Mehta PH (2016). A comparison of salivary testosterone measurement using immunoassays and tandem mass spectrometry. *Psychoneuroendocrinology*, 71, 180–188. 10.1016/j.psyneuen.2016.05.022. [PubMed: 27295182]
- Westman A, & Björnstig U (2007). Injuries in swedish skydiving. *British Journal of Sports Medicine*, 41(6), 356–364. 10.1136/bjsm.2006.031682. discussion 364 [PubMed: 17224436]
- Wilson LC, & Scarpa A (2014). Aggressive behavior: An alternative model of resting heart rate and sensation seeking. *Aggressive Behavior*, 40(1), 91–98. <https://doi.org/10.1002/ab.21504>. [PubMed: 23996463]
- Wobber V, Hare B, Maboto J, Lipson S, Wrangham R, & Ellison PT (2010). Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, 107(28), 12457–12462. 10.1073/pnas.1007411107. [PubMed: 20616027]
- Wranicz JK, Rosiak M, Cygankiewicz I, Kula P, Kula K, & Zareba W (2004). Sex steroids and heart rate variability in patients after myocardial infarction. *Annals of Noninvasive Electrophysiology: The Official Journal of the International Society for Holter and Noninvasive Electrophysiology, Inc*, 9(2), 156–161. 10.1111/.1542-474X.2004.92539.x.
- Zahn-Waxler C, Shirtcliff EA, & Marceau K (2008). Disorders of childhood and adolescence: Gender and psychopathology. *Annual Review of Clinical Psychology*, 4, 275–303. 10.1146/annurev.clinpsy.3.022806.091358.
- Zakreski E, Dismukes AR, Tountas A, Phan JM, Moody SN, & Shirtcliff EA (2019). Developmental trajectories of HPA-HPG dual axes coupling: Implications for social neuroendocrinology. *International handbook of social neuroendocrinology*. Abingdon, UK: Routledge.
- Zuckerman M (1979). *Sensation seeking; beyond the optimal level of arousal*. Hillsdale, NJ: Erlbaum.
- Zuckerman M (1990). The psychophysiology of sensation seeking. *Journal of Personality*, 58(1), 313–345. 10.1111/j.1467-6494.1990.tb00918.x. [PubMed: 2198341]
- Zuckerman M (1994). *Behavioral expressions and biosocial bases of sensation seeking*. New York: Cambridge University Press.
- Zuckerman M (2007). The sensation seeking scale V (SSS-V): Still reliable and valid. *Personality and Individual Differences*, 43(5), 1303–1305. 10.1016/j.paid.2007.03.021.

Fig. 1. Testosterone Response During Skydiving Relative to a Basal Day.

Significantly greater testosterone reactivity was observed during skydiving relative to a same-time comparison on a basal day.

Fig. 2. Predictors of Testosterone Reactivity during Skydiving.

The top left panel of Fig. 2 depicts logarithmically transformed testosterone levels in participants with high and low levels of sensation seeking. The bottom left panel of Fig. 2 depicts logarithmically transformed testosterone levels in participants with high and low levels of sympathetic nervous system activation as measured by area under the curve of heart rate. The top right panel of Fig. 2 depicts logarithmically transformed testosterone levels in participants with high and low levels of parasympathetic nervous system activation as measured by large area under the curve of the root mean square of successive differences. The bottom right panel of Fig. 2 illustrates that this is because participants with high tonic levels of parasympathetic activation showed significantly less testosterone on the basal day relative to participants with low tonic levels of parasympathetic response.

Fig. 3. Testosterone and Cortisol Show Coupling during Skydiving.

The left panel of Fig. 3 depicts the positive correlation between logarithmically transformed testosterone and cortisol levels during skydiving, while the right panel of Fig. 3 shows that increasing cortisol reactivity predicted increased testosterone reactivity during skydiving.

Table 1

Descriptive statistics for the sample.

		Min.	Max.	Mean	SD
Full Sample (N = 44)	Age	18.00	53.00	29.58	7.60
	Body Mass Index	16.71	32.81	24.65	3.59
	Sensation Seeking Scale-V	17.00	35.00	25.95	3.51
Reduced Sample (n = 36)	Age	18.00	47.00	29.03	7.02
	Body Mass Index	16.71	32.81	24.28	3.30
	Sensation Seeking Scale-V	17.00	31.00	25.77	3.24
	AUC ratio scores of Heart Rate	-1.62	2.00	-0.26	0.93
	AUC ratio scores of RMSSD	-1.37	2.00	-0.05	0.86

Note: Reduced sample is a sample size with the HR and RMSSD scores. AUC=area under the curve; RMSSD=root mean square of successive differences.

Table 2

Correlations Between Sensation Seeking Scale-V and Autonomic Measures (n = 36).

	1	2	3
1. SSS-V	-		
2. Heart Rate AUC	.042	-	
3. RMSSD	-.092	.033	-

Note: SSS-V = Sensation Seeking Scale-V; AUC = area under the curve; RMSSD = root mean square of successive differences.

Table 3

Regression coefficients of the most parsimonious models (N = 44).

	Gender Model	Maximum Cortisol Level	Cortisol Reactivity	Sensation Seeking Model	Sensation Seeking Model With Maximum Cortisol Level	Sensation Seeking Model With Cortisol Reactivity	Final Model
T Level	4.43***	4.39***	4.43***	4.43***	4.40***	4.44***	4.40***
Gender	-1.09***	-1.00***	-1.08***	-1.10***	-1.01***	-1.10***	-1.00***
Maximum Cortisol Level		0.43***			0.43***		0.51***
Level							
Basal Day T	0.28*	0.29*	0.26*	0.27*	0.29*	0.27*	0.28*
T reactivity	0.20***	0.20***	0.13***	0.20***	0.20***	0.19***	0.20***
Cortisol Reactivity			0.06*			0.06*	0.09***
SS Scale-V				0.01*	0.01*	0.01**	0.01**
T recovery	-0.20***	-0.20***	-0.20***	-0.20***	-0.20***	-0.20***	-0.21***
SS Scale-V				-0.01	-0.00	-0.01	-0.00
Basal day 'reactivity'	-0.21***	-0.21***	-0.22***	-0.22***	-0.22***	-0.23***	-0.24***
Basal day 'recovery'	0.26**	0.26**	0.29***	0.26**	0.26**	0.26**	0.26**

Note:

† $p < .10$ * $p < .05$ ** $p < .01$ *** $p < .001$.

HR=heart rate; RMSSD=root mean square of successive differences; Sensation Seeking=SS; T = Testosterone.

Table 4

Regression coefficients of the most parsimonious models (n = 36).

	Gender Model	Heart Rate Model	RMSSD Model	Heart Rate Model With RMSSD	Sensation Seeking Model	Sensation Seeking Model With Heart Rate	Sensation Seeking Model With RMSSD	Final Model
T Level	4.53***	4.54***	4.48***	4.48***	4.54***	4.48***	4.48***	4.48***
Gender	-1.19***	-1.18***	-1.11***	-1.12***	-1.19***	-1.12***	-1.13***	-1.13***
RMSSD reactivity			-0.34*	-0.33*		-0.34*	-0.33*	-0.33*
Basal Day T	0.20	0.19	0.23*	0.23*	0.19	0.23*	0.23*	0.23*
RMSSD reactivity			0.29*	0.29*		0.30*	0.30*	0.30*
T reactivity	0.21***	0.23***	0.21***	0.23***	0.24***	0.22***	0.22***	0.23***
HR reactivity		0.07*	0.06*	0.06*	0.07*		0.06*	0.06*
RMSSD reactivity			-0.11**	-0.10**		-0.10***	-0.10***	-0.10***
SS Scale-V					0.01*	0.01	0.01 [†]	0.01 [†]
T recovery	-0.18**	-0.20***	-0.19**	-0.20***	-0.21***	-0.20***	-0.21***	-0.21***
HR reactivity		-0.10**	-0.10*	-0.10*	-0.10*		-0.09 [†]	-0.09 [†]
SS Scale-V					-0.01**	-0.01*	-0.01*	-0.01*
Basal day 'reactivity'	-0.22**	-0.23***	-0.24***	-0.24***	-0.23***	-0.23***	-0.24***	-0.24***
Basal day 'recovery'	0.22*	0.27**	0.28**	0.27**	0.27**	0.28**	0.27**	0.27**

Note:

[†]p < .10

*p < .05

**p < .01

***p < .001.

HR = heart rate; RMSSD = root mean square of successive differences; Sensation Seeking = SS; T = Testosterone. HR and RMSSD reactivity indicate individual area-under-the-curve scores of the heart rate and the RMSSD after the jump of Skydiving, relative to these scores on the day of jump.