Psychopathic traits and reinforcement learning under acute stress

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Abstract

Objective: Individuals with high levels of psychopathic traits are often characterized by aberrant reinforcement learning. This type of learning, which implicates making choices that maximize rewards and minimize punishments, may be affected by acute stress. However, how acute stress affects reinforcement learning in individuals with different levels of psychopathic

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traits is not well-understood. Here, we investigated whether and how individual differences in psychopathic traits modulated the impact of acute stress on reward and punishment learning.

Method: Sixty-two male participants from a university sample completed the Self-Report Psychopathy-Short Form scale and performed a reinforcement-learning task involving monetary gains and losses whilst under acute stress and control conditions.

Results: Individual differences in psychopathic traits modulated the impact of acute stress on behavioral performance towards obtaining gains, but not towards avoiding losses. As levels of psychopathic traits increased, the impairing effect of acute stress on reward learning decreased. Specifically, acute stress impaired performance towards seeking gains to a larger extent in individuals with lower levels of psychopathic traits than in individuals with higher levels of these traits.

Conclusions: Our study indicates that psychopathic traits modulate the impact of acute stress on reward learning.

Keywords: Psychopathy; Reinforcement learning; Reward; Punishment; Stress

Introduction

Psychopathy is a personality disorder characterised by abnormal affective-interpersonal traits, such as lack of empathy and manipulativeness, and by deviant lifestyle-antisocial characteristics, such as impulsiveness and antisocial behavior (R. J. R. Blair et al., 2005; Hare, 2003; Hare & Neumann, 2008; Viding et al., 2014). Recent data suggests that psychopathic traits are continuously distributed in the general population (Neumann & Hare, 2008) and that individual differences in psychopathic traits in the general population can be mapped onto dysfunctional behavioral and neural processes systematically reported in individuals with a diagnosis of psychopathy (Seara-Cardoso & Viding, 2015).

Evidence from clinical populations suggests that psychopathy is associated with atypical reinforcement learning (K. S. Blair et al., 2006; R. J. R. Blair, 2013, 2017, 2019; R. J. R. Blair et al., 2005; Brazil et al., 2009; Brazil, Maes, et al., 2013; Budhani et al., 2006; Dargis et al., 2017; De Brito et al., 2013; Finger et al., 2011; Gregory et al., 2015; Newman & Kosson, 1986; Von Borries et al., 2010; White et al., 2013), which may ultimately result in maladaptive behavior (R. J. R. Blair, 2007, 2017; Brazil et al., 2011). Reinforcement learning implicates that individuals learn to select actions that maximize rewards and minimize punishments by gradually learning the values of those actions (Sutton & Barto, 1998). This requires the ability to learn from past actions: choices that result in rewards should be repeated, whereas choices that result in punishments should be avoided. Growing behavioral (K. S. Blair et al., 2006; R. J. R. Blair et al., 2004; Budhani et al., 2006; Dargis et al., 2017; De Brito et al., 2013; Newman & Kosson, 1986; Oba et al., 2019) and neural (R. J. R. Blair, 2013, 2019; Finger et al., 2011; Gregory et al., 2015; Pujara et al., 2014; Von Borries et al., 2010; White et al., 2013) data suggest that this ability to learn from past actions, and consequently choose between stimuli associated with rewards and/or punishments, is dysfunctional in psychopathy. This suggests that individuals with high psychopathic traits might have difficulties in learning to adjust their behaviors based on the rewarding and punishing outcomes of their choices. Despite the extant evidence, the extent to which different levels of psychopathic traits in the general population are associated with dysfunctional reinforcement learning remains more equivocal (Brazil, Hunt, et al., 2013; Oba et al., 2019). Furthermore, even less is known about whether and how situational factors, such as acute stress, may affect reinforcement learning in individuals with different levels of psychopathic traits.

Individuals often need to make choices, and learn from their outcomes, in non-ideal situations, such as when under acute stress. Acute stress, albeit ubiquitous in everyday life, is known to impact reinforcement learning in healthy individuals (Porcelli & Delgado, 2017). Accumulating evidence suggests that acute stress impairs reward learning (Berghorst et al., 2013; Bogdan et al., 2011; Bogdan & Pizzagalli, 2006; Carvalheiro et al., 2021b, 2021a; Cremer et al., 2021; de Berker et al., 2016; Morris & Rottenberg, 2015; Paret & Bublatzky, 2020) and punishment learning (de Berker et al., 2016; Petzold et al., 2010), although the evidence for the latter is less robust (Aylward et al., 2019; Carvalheiro et al., 2021b, 2021a; Porcelli & Delgado, 2017). Previous research indicates that individuals with high levels of psychopathic traits present blunted stress reactivity (Cima et al., 2008; Holi et al., 2006; House & Milligan, 1976; Johnson et al., 2015; Lidberg et al., 1978; Loney et al., 2006). The influential low-fear hypothesis theorizes that psychopathy is linked to a reduced ability to experience fear (Lykken, 1957) and, in particular, to deficits in automatic threat detection and responsivity (Hoppenbrouwers et al., 2016). Other studies propose that the blunted responding to threatful stimuli in individuals with psychopathy results from a deficit in their ability to reallocate attention to environmental stimuli once they are focused on a goal, such as obtaining rewards (Baskin-Sommers et al., 2012; Newman, 1998; Newman et al., 2010; Newman & Baskin-Sommers, 2012). As such, individuals with high psychopathic traits might be more insensitive to stimuli that typically induce acute stress, which, in turn, disrupt reinforcement-learning processes. Yet, little is known about whether psychopathic traits can interact with acute stress during reward and punishment learning.

In this study, we aimed to investigate the extent to which psychopathic traits modulated the impact of acute stress on reinforcement learning. We used an existing data set originally collected to assess how acute stress affects reward and punishment learning (Carvalheiro et al., 2021b). Participants performed a well-established reinforcement-learning task (Pessiglione et al., 2006) involving monetary gains (i.e., rewards) and losses (i.e., punishments), whilst under acute stress and control conditions (Figure 1), and completed the Self-Report Psychopathy-Short Form [(Paulhus et al., 2016); Portuguese version (Seara-Cardoso et al., 2020)]. To provide a more comprehensive understanding of the role of psychopathic traits in modulating the impact of acute stress on reward and punishment learning, we also explored the contribution of each dimension of psychopathy (affective-interpersonal and lifestyle-antisocial) (Hare, 2003; Hare & Neumann, 2008). To assess acute stress responses, we collected self-reported stress levels and skin conductance response measures.

Considering that psychopathic traits have been associated with both abnormal reinforcement learning and atypical stress responsivity, we hypothesized that psychopathic traits would modulate the impact of acute stress on reward and punishment learning. Specifically, given that acute stress is thought to impair reinforcement learning and that psychopathy has been characterized by reduced stress responsivity, we expected that the impairing effect of acute stress on reward and punishment learning effect of acute stress on reward and punishment learning would decrease as psychopathic traits increased.

Materials & Methods

Participants

Sixty-two male healthy participants (age range = 18-35; M = 21.9, SD = 3.7) were recruited at University of Minho. Only male participants were recruited to avoid the potential confounding effect of females' menstrual-cycle-dependent variation on stress responsivity (Ossewaarde et al., 2010) and on reward/punishment learning (Diekhof & Ratnayake, 2016; Dreher et al., 2007). No participants were excluded from data analyses, although we conducted confirmatory analyses excluding potential outliers to ensure that our results were not driven by extreme values. Participants provided informed consent before the experimental session. All experimental procedures were approved by the Ethics Committee of University of Minho. A study on this sample focusing on the effects of acute stress on reward learning, without consideration of individual differences in psychopathic traits, has been recently made available (Carvalheiro et al., 2021b).

Self-Report Psychopathy-Short Form (SRP-SF)

The Self-Report Psychopathy-Short Form [SRP-SF; (Paulhus et al., 2016); Portuguese version (Seara-Cardoso et al., 2020)] is a 29-item questionnaire assessing psychopathic traits. The instrument follows the same factor structure as the Psychopathy Checklist–Revised (Hare, 2003) and assesses four facets of psychopathy — affective, interpersonal, lifestyle, antisocial — which can also be modeled in terms of the traditional two-factor dimensions of psychopathy: affective-interpersonal and lifestyle-antisocial. Items are answered on a 5-point Likert scale that ranges from 1 (disagree strongly) to 5 (agree strongly). Scores of each dimension are obtained by summing up the corresponding individual item scores. The affective-interpersonal dimension taps the affective aspects of psychopathy, such as compromised empathy or lack of guilt and concern about others (e.g., "I never feel guilty over hurting others" and "People sometimes say that I'm cold-hearted"),

and interpersonal and dissocial characteristics, such as pathological lying and manipulation (e.g., "I would get a kick out of scamming someone", and "I have pretended to be someone else in order to get something"). The lifestyle-antisocial dimension relates to impulsive (e.g., "I admit that I often mouth off without thinking" and "I've often done something dangerous just for the thrill of it") and antisocial behaviors (e.g., "I have threatened people into giving me money, clothes, or makeup" and "I was convicted of a serious crime"). The antisocial subscale includes eight items, but only seven items are considered, as the item "gang activity" is omitted in community samples due to its low variability, as is the case of the current sample. The other subscales are also composed of seven items, resulting in 14 items in each dimension. Therefore, SRP-SF scores were computed from a total of 28 items.

Overall, the distributions of the levels of psychopathic traits measured by the SRP-SF in the current sample were consistent with other published studies on the SRP-SF with large samples (Gordts et al., 2017; Seara-Cardoso et al., 2020) (Table 1; see also Figure S1 in the Supplemental Material for histograms with the distribution of psychopathic traits in our sample). Calculation of the Chronbach's alpha showed adequate reliability of the SRP-SF total scale ($\alpha = 0.87$) and both dimension subscales (affective-interpersonal, $\alpha = 0.81$; lifestyle-antisocial, $\alpha = 0.75$). The two dimensions were significantly correlated ($r_s = 0.65$, p < 0.001).

Table 1. Descriptive statistics (Mean and Standard deviation, Median and Minimum andMaximum values) of Self-Report Psychopathy-Short Form (SRP-SF) total scores and dimensions(affective-interpersonal and lifestyle-antisocial).

	Total	Dimensions	
		Affective-	Lifestyle-
		interpersonal	antisocial
Mean (SD)	53.73 (12.74)	29.00 (7.84)	24.73 (5.99)
Median [Min, Max]	53 [34, 95]	27.5 [16, 54]	25 [15, 41]

Reinforcement-learning task

Participants completed four blocks of an adapted version of a well-established reinforcement-learning task (Pessiglione et al., 2006), as comprehensively described in Carvalheiro et al.,
(2021b). Each block included three pairs of abstract stimuli, and each pair of stimuli was presented 40 times, resulting in 120 trials per block, 480 trials per participant, and a total of 29760 possible

responses across all participants (n = 62). In each trial, participants were asked to choose between two abstract visual stimuli so as to maximize gains and minimize losses. Each pair of stimuli was associated with a valence: one pair of stimuli was associated with gains (+0.5€ or nothing), a second pair was associated with losses (-0.5€ or nothing), and a third pair was associated with neutral, or non-monetary outcomes (look at a 0.5€ coin or nothing). The pairs of stimuli were presented in a pseudo-randomized order within each block, and different stimuli were used in each block. The two outcome probabilities were reciprocally 0.8 and 0.2 for the stimuli in each of the three pairs (Figure 1). That is, in gain trials, one stimulus was associated with a probability of 0.8 of winning 0.5€ and with a probability of 0.2 of winning nothing ("correct" stimulus), and the other stimulus was associated with a probability of 0.2 of winning 0.5€ and with a probability of 0.8 of winning nothing ("incorrect" stimulus); in loss trials, one stimulus was associated with a probability of 0.8 of losing 0.5€ and with a probability of 0.2 of losing nothing ("incorrect" stimulus), and the other stimulus was associated with a probability of 0.2 of losing 0.5€ and with a probability of 0.8 of losing nothing ("correct" stimulus). These outcome probabilities remained constant within each block. Given that neutral trials were not associated with monetary outcomes, and thus there were no correct/incorrect responses during neutral trials (performance during neutral trials did not differ significantly from chance level in both conditions, p > 0.15), we did not analyze participants performance during this type of trial, meaning that our analyses included 2/3of the trials, i.e., gain and loss trials.

Participants were informed that they would be paid the amount obtained during a randomly selected block, but they all left with the same fixed amount (15€). The experiment was programmed and presented with Cogent 2000 (http://www.vislab.ucl.ac.uk/cogent.php) implemented in MATLAB R2015a (MathWorks).

Figure 1. Reinforcement-learning task. On each trial, participants chose either the upper or the lower of two abstract visual stimuli and subsequently observed the outcome of their choice, whilst



under acute stress and control conditions. (a) In the stress-condition example, the chosen stimulus was associated with a probability of 0.8 of winning $0.5 \in$ and with a probability of 0.2 of winning nothing. (b) In the control-condition example, the chosen stimulus was associated with a probability of 0.8 of losing $0.5 \in$ and with a probability of 0.2 of losing nothing.

Acute-stress manipulation

During the experimental session, participants performed two blocks of the reinforcement-learning task whilst exposed to a stressor (i.e., stress condition; Figure 1a) and two blocks without the stressor (i.e., control condition; Figure 1b). To elicit stress responses, we exposed participants to an auditory stimulus: a predictable, but uncontrollable, sound alarm. Stress blocks were signaled by a warning sign and a red background (Figure 1a), and control blocks were signaled by a safe sign and blue background (Figure 1b). Stress and control blocks were administered alternately and in a counterbalanced order. To check the success of the acute-stress manipulation, we collected self-report stress levels at the end of each block of the task and measured skin conductance response (SCR) rate throughout the task. In a previous study, using the same dataset, we confirmed that participants reported higher stress levels and exhibited augmented skin-conductance response rate in the stress condition compared with the control condition (Carvalheiro et al., 2021b).

To assess how psychopathic traits were associated with stress responsivity, we correlated psychopathic traits with the difference in self-reported stress levels and SCR rate (averaged across blocks) between the stress and control conditions. We performed Spearman correlations, which are more robust to extreme values. To assess whether the correlations for each dimension were significantly different from each other, we applied the Meng's et al., (1992) approach using the "cocor" package in R (http://www.r-project.org).

Task performance analyses

To examine how psychopathic traits modulated the impact of acute stress on choice performance during the reinforcement-learning task, we applied generalized linear mixed-effects (glme) models to participants' trial-by-trial choice data (with correct and incorrect choices coded as 1 and 0). We used a "logit" link function to account for the binomial distribution of the data. As predictor variables in the glme models, we included individual psychopathic traits (continuous SRP-SF scores), condition (0 or 1 for control and stress conditions, respectively), valence (0 or 1 for loss

and gain trials, respectively), block number (0 or 1, for blocks 1 and 2, respectively), and trial number (1 to 40), and tested the interactions between SRP-SF scores, condition, and valence. Block and trial number were included as covariates of noninterest to control for potential temporal effects. We included by-subject random intercepts and by-subject random slopes for all predictor variables (condition, valence, block, and trial).

We generated a glme model to assess the interaction between SRP-SF total scores, condition, and valence, and two other glme models to assess the interaction between SRP-SF scores in each dimension of psychopathy (affective-interpersonal and lifestyle-antisocial), condition, and valence. We fitted the glme models to the behavioral data using the "lme4" package in R (http://www.r-project.org), and we used the "ggpredict" function to obtain the logit-glme-model-predicted probability of choosing the "correct" stimulus (i.e., the stimulus associated with a 0.8 probability of winning in gain trials and the stimulus associated with a 0.2 probability of losing in loss trials). To further understand the nature of the interactions, we performed simple slope and Johnson-Neyman analyses using the "interactions" package in R. Simple slope analyses tested the significance of the associations between SRP-SF scores and behavioral performance during gain or loss trials in each condition, and Johnson-Neyman analyses detected the ranges of values of SRP-SF scores for which the interaction effect was significant (p < 0.05). To test for potential differences between the associations involving each of the psychopathy dimensions, we compared the regression coefficients (i.e., slopes) of the interactions obtained from the analysis of each dimension (Paternoster et al., 1998).

As performance below chance could be indicative of non-compliance with the experimental setting, we inspected whether the percentage of correct answers across gain and loss trials was lower than 50% in the stress or control conditions. We repeated the analyses excluding the three participants who performed below chance levels. Additionally, we identified one participant with "extreme" (± 3 standard deviations from the mean) SRP-SF scores (SRP-SF total = 95) and repeated the analyses excluding that participant to confirm that the results were not driven by extreme values. Given the two distinct criteria (i.e., performance below chance and extreme SRP-SF scores), we performed these additional checks in two independent steps.

Results

First, we inspected how total psychopathic traits modulated the impact of acute stress on behavioral performance towards monetary gains and losses (see Figures S2 and S3 in the Supplemental Material for a distribution of the percentage of correct answers in gain and loss trials, respectively, across psychopathic traits). We found a significant interaction between SRP-SF total scores, condition, and valence ($\beta = 0.028$, p < 0.001, 95% confidence interval (CI) = [0.012, 0.042]; Figure 2a). To better understand the nature of this interaction, we performed simple slope and Johnson-Neyman analyses. Simple slope analyses did not show any significant results (p > 0.22). However, Johnson-Neyman analyses detected that the effect of condition was significant in gain trials, but not in loss trials, when SRP-SF total scores were lower than 54.07 (representing 56% of the sample). This indicates that the negative effect of acute stress on performance towards gains was more pronounced in individuals with lower levels of psychopathic traits than in individuals with higher levels of these traits (Figure 2a).

Second, to better understand the extent to which each dimension of SRP-SF — affectiveinterpersonal and lifestyle-antisocial — modulated the impact of acute stress on task performance in gain and loss trials, we conducted new glme models including the SRP-SF scores on each dimension as predictor variables. We found a significant interaction between affectiveinterpersonal traits, condition, and valence ($\beta = 0.033$, p = 0.0075, 95% CI = [0.00089, 0.058]; Figure 2b). Simple slope analyses were all non-significant (p > 0.18). However, Johnson-Neyman analyses detected that the slope of condition was significant in gain trials, but not in loss trials, when affective-interpersonal scores were lower than 30.12 (representing 56% of the sample). We also found a significant interaction between lifestyle-antisocial traits, condition, and valence ($\beta =$ 0.060, p < 0.001, 95% CI = [0.029, 0.090]; Figure 2c). Again, simple slope analyses were all nonsignificant (p > 0.11), but Johnson-Neyman analyses detected that the effect of condition was significant in gain trials, but not in loss trials, when lifestyle-antisocial scores were lower than 25.44 (representing 56% of the sample). In Johnson-Neyman analyses, the cutoff for statistical significance coincided with 56% of the sample for the three different sets of psychopathy scores, which might be related with the high intercorrelations between the psychopathy scores ($0.65 < r_s < 0.94$, all p < 0.001). The above interactions for affective-interpersonal and lifestyle-antisocial traits were not significantly different (Z = -1.35, p = 0.18). These results indicate that acute stress had a



stronger negative effect on the performance towards obtaining gains in individuals with low traits in both the affective-interpersonal and lifestyle-antisocial dimensions of psychopathy than in individuals with higher levels of these traits (Figures 2b and 2c).

Figure 2. Percentage of correct gain (left) and loss (right) choices in the stress (red) and control (blue) conditions estimated by the generalized linear mixed-effects models across Self-Report Psychopathy-Short Form (SRP-SF) (a) total, (b) affective-interpersonal, and (c) lifestyle-antisocial scores (b and c correspond to the SRP-SF dimensions). The central lines depict the logit-model-predicted probabilities and the shading around those central lines represents 95% confidence intervals. The slopes (β) and p-values adjacent to the lines were obtained through simple slope analyses for each condition (stress and control) and valence (gains and losses). Shaded gray areas were obtained through Johnson-Neyman analyses and identify the ranges of values of SRP-SF scores for which the interaction is significant (p < 0.05).

Given that three participants performed below chance levels, we repeated the aforementioned analyses excluding those three participants to ensure that our results were robust. After excluding those participants, the significance of the interactions (all interactions between SRP-SF scores, condition, and valence; p < 0.038) and the interpretation of Johnson-Neyman regions of significance remained unchanged (the effect of condition was significant in gain trials when SRP-SF total scores < 62.21, affective-interpersonal scores < 31.00, and lifestyle-antisocial scores < 29.23). Moreover, we excluded one participant who scored very high on the SRP-SF (i.e., more than 3 standard deviations above from the mean; SRP-SF total score = 95); once again, the interpretation of the interactions (all interactions between SRP-SF scores, condition, and valence; p < 0.048) and Johnson-Neyman regions of significance remained unchanged (the effect of condition was significant in gain trials when SRP-SF total scores < 54.43, affective-interpersonal scores < 29.51, and lifestyle-antisocial scores < 25.30).

For completeness, we assessed how different levels of psychopathic traits were associated with stress responsivity. For this, we used the difference in self-reported stress levels and SCR rate between the stress and control conditions as a proxy for stress responsivity. We identified a trend for a negative association between SRP-SF total scores and self-reported stress responsivity, although the correlation was non-significant ($r_s = -0.22$, p = 0.091; Figure S4). Inspection of the dimensions of psychopathy showed a significant negative association between lifestyle-antisocial and self-reported stress responsivity ($r_s = -0.23$, p = 0.019), but not between affective-interpersonal traits and self-reported stress responsivity ($r_s = -0.15$, p = 0.25). However, these two correlations for the dimensions of psychopathy were not significantly different (Z = -1.42, p = 0.16). We did

not find any associations between psychopathic traits and the SCR rate (-0.074 $< r_s <$ -0.012, all p < 0.58).

Discussion

In this study, we investigated whether and how individual differences in psychopathic traits modulated reinforcement learning under acute stress. We used a multidimensional measure of psychopathy and a reinforcement-learning task combined with a stress induction, to examine how psychopathic traits modulated the impact of acute stress on both reward and punishment learning. We found that psychopathic traits modulated the impact of acute stress on behavioral performance towards monetary rewards, but not punishments. More specifically, acute stress impaired behavioral performance towards rewards in individuals with lower levels of psychopathic traits to a larger extent than in individuals with higher levels of psychopathic traits. That is, as levels of psychopathic traits increased, the impairing effect of acute stress on reward learning decreased. This effect was observed across the affective-interpersonal and lifestyle-antisocial dimensions of psychopathy, suggesting a modulatory role of global psychopathic traits on reward learning under acute stress.

According to the response-modulation hypothesis, psychopathic individuals demonstrate difficulties in reallocating attention to environmental stimuli once they are focused on a goal, such as seeking rewards (Baskin–Sommers et al., 2012; Hamilton & Newman, 2018; Newman, 1998; Newman et al., 2010; Newman & Baskin-Sommers, 2012; Newman & Kosson, 1986; Smith & Lilienfeld, 2015). Whereas in healthy individuals, attention is shifted periodically to attend to environmental stimuli, such as threatful stimuli or stressors, it has been proposed that individuals with psychopathy might be unable to shift their attention to such peripheral stimuli unrelated to their main goal, particularly if that goal involves obtaining rewards. This model could explain, at least partially, why the impairing effect of acute stress on reward learning decrease as psychopathic traits increase.

Interestingly, our data suggest a selective modulatory effect of psychopathic traits on the impact of acute stress on reward learning, but not punishment avoidance learning. The effects of acute stress on punishment learning are generally less well-understood (Porcelli & Delgado, 2017). Previous behavioral studies suggest that acute stress impairs reward learning, but the evidence for stress-induced deficits in punishment learning is scarcer (Berghorst et al., 2013; Carvalheiro et al., 2021b, 2021a; Porcelli & Delgado, 2017). Reward learning has been robustly

associated with dopaminergic functioning (Daw & Tobler, 2014; Glimcher, 2011; Pessiglione et al., 2006; Schultz et al., 1997), and it is known that acute stress increases dopamine release (Adler et al., 2000; Cabib & Puglisi-Allegra, 2012; Pruessner et al., 2004), which in turn might affect this type of learning. Psychopathic traits have been associated with dopaminergic disturbances (Buckholtz et al., 2010; Yildirim & Derksen, 2015). For example, Buckholtz et al. (2010) showed that psychopathic traits in a community sample were associated with a hyper-reactive dopaminergic reward system. It is possible that this enhanced dopaminergic functioning interacts with stress-induced dopamine release thus leading to a modulation of the effect of stress in reward learning. The involvement of dopaminergic functioning on punishment learning is more poorly understood (Glimcher, 2011; Pessiglione et al., 2006), suggesting that stress-induced dopamine release might not affect punishment learning to the same extent as it affects reward learning. Our results are consistent with this hypothesis; if reward learning is impaired by acute stress via dopaminergic mechanisms, that might explain why psychopathic traits selectively modulate the effect of acute stress on reward learning.

Our results did not provide support for an association between psychopathy scores and performance towards obtaining rewards and/or avoiding punishments in the control condition. This is interesting and may seem at odds with previous behavioral literature, which suggests that psychopathy is characterized by deficits in reward and, more markedly, in punishment learning (K. S. Blair et al., 2006; R. J. R. Blair et al., 2005; R. J. R. Blair & Mitchell, 2009). However, closer inspection of these studies shows important differences in the type of learning deficits identified. Previous studies found robust evidence of learning deficits in passive avoidance of punishments (R. J. R. Blair et al., 2004; De Brito et al., 2013; Finger et al., 2011; Newman & Kosson, 1986; Newman & Schmitt, 1998), a form of classic conditioning which requires the formation of stimulus-punishment associations but no action execution, and in reversal learning (Brazil, Maes, et al., 2013; Budhani et al., 2006; Dargis et al., 2017; De Brito et al., 2013; Gregory et al., 2015; Mitchell et al., 2002), which occurs when previously learned reward/punishment contingencies are reversed. There is less evidence of impaired stimulus – response associations in the early, gradual learning of actions that lead to rewards/punishments (Brazil, Maes, et al., 2013; Budhani et al., 2006; Dargis et al., 2017; De Brito et al., 2013; Mitchell et al., 2002), which is the type of learning assessed by our task. Thus, it is possible that psychopathy is not characterized by deficits in all types of reinforcement learning (R. J. R. Blair et al., 2005).

Previous evidence indicates that, even at relatively low levels, psychopathic traits can be pathological (Neumann & Hare, 2008) and associated with atypical behavioral and neural processes (Seara-Cardoso & Viding, 2015). Studies focused on the normative variation in psychopathic traits can thus provide important insights into the broader phenotypic variability found across the dimensional distribution of psychopathic traits (Guay et al., 2007). Using a normative sample, we were able to capture broader variability in psychopathic traits, although we cannot exclude the possibility that additional associations between psychopathic traits, reward and/or punishment learning, and acute stress could have emerged in a sample that included individuals at the higher end of the distribution.

Limitations

Reduced stress responsivity in psychopathy has been typically indexed by levels of cortisol (Cima et al., 2008; Holi et al., 2006; Johnson et al., 2015; Loney et al., 2006; Thompson et al., 2014), a steroid hormone which mediates the stress response (Joëls & Baram, 2009). Although our task design precluded the measurement of cortisol levels, we assessed whether psychopathic traits were associated with differences in self-reported stress levels and/or SCR rate between stress and control conditions. Our findings indicated that the difference in self-reported stress levels tended to decrease as psychopathic traits increased but we did not find evidence for an association between psychopathic traits and the difference in SCR rate. This is at odds with previous literature (Arnett, 1997; Boucsein, 2012; Lorber, 2004). However, skin conductance hypoactivity for negative stimuli in psychopathy seems to appear more clearly for tonic skin conductance levels or for the amplitude of event-specific skin conductance responses (e.g., anticipatory response to punishment stimuli), rather than for the rate of non-specific, phasic SCRs (Arnett, 1997; Boucsein, 2012), as measured during our task. Future studies in both clinical and non-clinical populations should assess how stress responsivity (subjective and physiological) modulates the impact of acute stress on reinforcement learning across the spectrum of psychopathy.

In this study, we included only male participants due to females' hormonal-dependent variations on stress responsivity (Ossewaarde et al., 2010), as well as on reward and punishment learning (Diekhof & Ratnayake, 2016; Dreher et al., 2007). Further studies are needed to assess whether women with high levels of psychopathic traits are also characterized by a decreased impairment of reward learning under acute stress.

Finally, it remains debatable whether the putative protective role of psychopathic traits against the impairing effect of acute stress on reward, but not punishment avoidance, learning is associated with maladaptive behaviors under acute stress. Future studies could assess how stressinduced task performance variability across the spectrum of psychopathy relates to real-life behavior, by collecting measures of criminal behavior or substance use, for example, which are often associated with psychopathy. Computational modeling studies in large community and clinical samples could further contribute for a better understanding of altered reinforcementlearning mechanisms, and how acute stress interacts with those mechanisms, in psychopathy.

Conclusions

We present evidence that psychopathic traits modulate the impact of acute stress on reward learning, but not on punishment learning. Our findings suggest that the impairing effect of acute stress on reward learning decreases as the levels of psychopathic traits increase, such that acute stress impaired reward learning in individuals with lower psychopathic traits, but such stressinduced impairment was not observed in individuals with higher levels of these traits. Thus, our data suggest that psychopathic traits may protect against the deleterious impact of acute stress on reward learning and that impaired reinforcement learning associated with psychopathy may depend not only on the type of learning but also on situational factors, such as acute stress.

This study highlights the substantial variability in how individuals learn from rewards under acute stress and the importance of considering individual differences that may contribute for such variability. Understanding how individual differences in psychopathic traits modulate the extent to which individuals learn from the outcomes of their choices under stressful conditions could pave the way to better characterize the interplay between psychopathy, emotional states, and decision-making.

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References

- Adler, C. M., Elman, I., Weisenfeld, N., Kestler, L., Pickar, D., & Breier, A. (2000). Effects of acute metabolic stress on striatal dopamine release in healthy volunteers. *Neuropsychopharmacology*, 22(5), 545–550. https://doi.org/10.1016/S0893-133X(99)00153-0
- Arnett, P. A. (1997). Autonomic responsivity in psychopaths: A critical review and theoretical proposal. *Clinical Psychology Review*, *17*(8), 903–936. https://doi.org/10.1016/S0272-7358(97)00045-7
- Aylward, J., Valton, V., Ahn, W.-Y., Bond, R. L., Dayan, P., Roiser, J. P., & Robinson, O. J.
 (2019). Altered learning under uncertainty in unmedicated mood and anxiety disorders. *Nature Human Behaviour*, *3*(10), 1116–1123. https://doi.org/10.1038/s41562-019-0628-0
- Baskin–Sommers, A., Curtin, J. J., Li, W., & Newman, J. P. (2012). Psychopathy-related differences in selective attention are captured by an early event-related potential. *Personality disorders*, *3*(4), 370–378. https://doi.org/10.1037/a0025593
- Berghorst, L. H., Bogdan, R., Frank, M. J., & Pizzagalli, D. A. (2013). Acute stress selectively reduces reward sensitivity. *Frontiers in Human Neuroscience*, 7(133). https://doi.org/10.3389/fnhum.2013.00133
- Blair, K. S., Morton, J., Leonard, A., & Blair, R. J. R. (2006). Impaired decision-making on the basis of both reward and punishment information in individuals with psychopathy.
 Personality and Individual Differences, 41(1), 155–165.
 https://doi.org/10.1016/j.paid.2005.11.031
- Blair, R. J. R. (2007). The amygdala and ventromedial prefrontal cortex in morality and psychopathy. *Trends in Cognitive Sciences*, *11*(9), 387–392. https://doi.org/10.1016/j.tics.2007.07.003
- Blair, R. J. R. (2013). The neurobiology of psychopathic traits in youths. *Nature Reviews Neuroscience*, 14(11), 786–799. https://doi.org/10.1038/nrn3577
- Blair, R. J. R. (2017). Emotion-based learning systems and the development of morality. *Cognition*, 167, 38–45. https://doi.org/10.1016/j.cognition.2017.03.013

- Blair, R. J. R. (2019). Dysfunctional neurocognition in individuals with clinically significant psychopathic traits. *Dialogues in Clinical Neuroscience*, *21*(3), 291–299. https://doi.org/10.31887/DCNS.2019.21.3/rblair
- Blair, R. J. R., Mitchell, D., & Blair, K. S. (2005). *The Psychopath: Emotion and the Brain*.Oxford: Blackwell Publishing.
- Blair, R. J. R., & Mitchell, D. G. V. (2009). Psychopathy, attention and emotion. *Psychological Medicine*, 39(4), 543–555. https://doi.org/10.1017/S0033291708003991
- Blair, R. J. R., Mitchell, D. G. V., Leonard, A., Budhani, S., Peschardt, K. S., & Newman, C. (2004). Passive avoidance learning in individuals with psychopathy: Modulation by reward but not by punishment. *Personality and Individual Differences*, *37*(6), 1179–1192. https://doi.org/10.1016/j.paid.2003.12.001
- Bogdan, R., & Pizzagalli, D. A. (2006). Acute stress reduces reward responsiveness: Implications for depression. *Biological Psychiatry*, *60*(10), 1147–1154.
 https://doi.org/10.1016/j.biopsych.2006.03.037
- Bogdan, R., Santesso, D. L., Fagerness, J., Perlis, R. H., & Pizzagalli, D. A. (2011). Corticotropinreleasing hormone receptor type 1 (CRHR1) genetic variation and stress interact to influence reward learning. *The Journal of Neuroscience*, *31*(37), 13246–13254. https://doi.org/10.1523/JNEUROSCI.2661-11.2011
- Boucsein, W. (2012). *Electrodermal activity* (2nd ed.). Springer. https://doi.org/10.1007/978-1-4614-1126-0
- Brazil, I. A., de Bruijn, E. R. A., Bulten, B. H., von Borries, A. K. L., van Lankveld, J. J. D. M.,
 Buitelaar, J. K., & Verkes, R. J. (2009). Early and late components of error monitoring in violent offenders with psychopathy. *Biological Psychiatry*, 65(2), 137–143.
 https://doi.org/10.1016/j.biopsych.2008.08.011
- Brazil, I. A., Hunt, L. T., Bulten, B. H., Kessels, R. P. C., de Bruijn, E. R. A., & Mars, R. B. (2013). Psychopathy-related traits and the use of reward and social information: A computational approach. *Frontiers in Psychology*, *4*(952). https://doi.org/10.3389/fpsyg.2013.00952
- Brazil, I. A., Maes, J. H. R., Scheper, I., Bulten, B. H., Kessels, R. P. C., Verkes, R. J., & de Bruijn, E. R. A. (2013). Reversal deficits in individuals with psychopathy in explicit but not implicit learning conditions. *Journal of Psychiatry and Neuroscience*, *38*(4), E13–E20. https://doi.org/10.1503/jpn.120152

- Brazil, I. A., Mars, R. B., Bulten, B. H., Buitelaar, J. K., Verkes, R. J., & De Bruijn, E. R. A.
 (2011). A neurophysiological dissociation between monitoring one's own and others' actions in psychopathy. *Biological Psychiatry*, 69(7), 693–699. https://doi.org/10.1016/j.biopsych.2010.11.013
- Buckholtz, J. W., Treadway, M. T., Cowan, R. L., Woodward, N. D., Benning, S. D., Li, R.,
 Ansari, M. S., Baldwin, R. M., Schwartzman, A. N., Shelby, E. S., Smith, C. E., Cole, D.,
 Kessler, R. M., & Zald, D. H. (2010). Mesolimbic dopamine reward system
 hypersensitivity in individuals with psychopathic traits. *Nature Neuroscience*, *13*(4), 419–421. PubMed. https://doi.org/10.1038/nn.2510
- Budhani, S., Richell, R. A., & Blair, R. J. R. (2006). Impaired reversal but intact acquisition:
 Probabilistic response reversal deficits in adult individuals with psychopathy. *Journal of Abnormal Psychology*, *115*(3), 552–558. https://doi.org/10.1037/0021-843X.115.3.552
- Cabib, S., & Puglisi-Allegra, S. (2012). The mesoaccumbens dopamine in coping with stress.
 Neuroscience and Biobehavioral Reviews, *36*(1), 79–89. https://doi.org/10.1016/j.neubiorev.2011.04.012
- Carvalheiro, J., Conceição, V. A., Mesquita, A., & Seara-Cardoso, A. (2021a). Acute stress blunts prediction error signals in the dorsal striatum during reinforcement learning. *bioRxiv*. https://doi.org/10.1101/2021.02.11.430640
- Carvalheiro, J., Conceição, V. A., Mesquita, A., & Seara-Cardoso, A. (2021b). Acute stress impairs reward learning in men. *Brain and Cognition*, 147, 105657. https://doi.org/10.1016/j.bandc.2020.105657
- Cima, M., Smeets, T., & Jelicic, M. (2008). Self-reported trauma, cortisol levels, and aggression in psychopathic and non-psychopathic prison inmates. *Biological Psychology*, *78*(1), 75–86. https://doi.org/10.1016/j.biopsycho.2007.12.011
- Cremer, A., Kalbe, F., Gläscher, J., & Schwabe, L. (2021). Stress reduces both model-based and model-free neural computations during flexible learning. *NeuroImage*, 117747. https://doi.org/10.1016/j.neuroimage.2021.117747
- Dargis, M., Wolf, R. C., & Koenigs, M. (2017). Reversal learning deficits in criminal offenders:
 Effects of psychopathy, substance use, and childhood maltreatment history. *Journal of Psychopathology and Behavioral Assessment*, 39(2), 189–197.
 https://doi.org/10.1007/s10862-016-9574-6

- Daw, N. D., & Tobler, P. N. (2014). Value learning through reinforcement: The basics of dopamine and reinforcement learning. In P. W. Glimcher & E. Fehr (Eds.), *Neuroeconomics: Decision Making and the Brain* (2nd ed., pp. 283–298). Elsevier Inc. http://www.sciencedirect.com/science/article/pii/B9780124160088000152
- de Berker, A. O., Tirole, M., Rutledge, R. B., Cross, G. F., Dolan, R. J., & Bestmann, S. (2016).
 Acute stress selectively impairs learning to act. *Scientific Reports*, *6*, 29816.
 https://doi.org/10.1038/srep29816
- De Brito, S. A., Viding, E., Kumari, V., Blackwood, N., & Hodgins, S. (2013). Cool and hot executive function impairments in violent offenders with antisocial personality disorder with and without psychopathy. *PLoS ONE*, 8(6). https://doi.org/10.1371/journal.pone.0065566
- Diekhof, E. K., & Ratnayake, M. (2016). Menstrual cycle phase modulates reward sensitivity and performance monitoring in young women: Preliminary fMRI evidence. *Neuropsychologia*, 84, 70–80. https://doi.org/10.1016/j.neuropsychologia.2015.10.016
- Dreher, J.-C., Schmidt, P. J., Kohn, P., Furman, D., Rubinow, D., & Berman, K. F. (2007). Menstrual cycle phase modulates reward-related neural function in women. *Proceedings of the National Academy of Sciences*, *104*(7), 2465–2470. https://doi.org/10.1073/pnas.0605569104
- Finger, E. C., Marsh, A. A., Blair, K. S., Reid, M. E., Sims, C., Ng, P., Pine, D. S., & Blair, R. J. R. (2011). Disrupted reinforcement signaling in the orbitofrontal cortex and caudate in youths with conduct disorder or oppositional defiant disorder and a high level of psychopathic traits. *American Journal of Psychiatry*, *168*(2), 152–162. https://doi.org/10.1176/appi.ajp.2010.10010129
- Glimcher, P. W. (2011). Understanding dopamine and reinforcement learning: The dopamine reward prediction error hypothesis. *Proceedings of the National Academy of Sciences*, *108*(Supplement 3), 15647. https://doi.org/10.1073/pnas.1014269108
- Gordts, S., Uzieblo, K., Neumann, C., Bussche, E. V. D., & Rossi, G. (2017). Validity of the Self-Report Psychopathy Scales (SRP-III full and short versions) in a community sample.
 Assessment, 24(3), 308–325. https://doi.org/10.1177/1073191115606205
- Gregory, S., Blair, R. J. R., Ffytche, D., Simmons, A., Kumari, V., Hodgins, S., & Blackwood, N.(2015). Punishment and psychopathy: A case-control functional MRI investigation of

reinforcement learning in violent antisocial personality disordered men. *The Lancet Psychiatry*, 2(2), 153–160. https://doi.org/10.1016/S2215-0366(14)00071-6

- Guay, J.-P., Ruscio, J., Knight, R. A., & Hare, R. D. (2007). A taxometric analysis of the latent structure of psychopathy: Evidence for dimensionality. *Journal of Abnormal Psychology*, *116*(4), 701–716. https://doi.org/10.1037/0021-843X.116.4.701
- Hamilton, R. B., & Newman, J. P. (2018). The response modulation hypothesis: Formulation, development, and implications for psychopathy. In *Handbook of psychopathy* (2nd ed., pp. 80–93). The Guilford Press.
- Hare, R. D. (2003). The Hare Psychopathy Checklist Revised (2nd ed.). Multi-Health Systems.
- Hare, R. D., & Neumann, C. S. (2008). Psychopathy as a clinical and empirical construct. *Annual Review of Clinical Psychology*, 4(1), 217–246.
 https://doi.org/10.1146/annurev.clinpsy.3.022806.091452
- Holi, M., Auvinen-Lintunen, L., Lindberg, N., Tani, P., & Virkkunen, M. (2006). Inverse correlation between severity of psychopathic traits and serum cortisol levels in young adult violent male offenders. *Psychopathology*, *39*(2), 102–104. https://doi.org/10.1159/000091021
- Hoppenbrouwers, S. S., Bulten, Berend H., & Brazil, Inti A. (2016). Parsing fear: A reassessment of the evidence for fear deficits in psychopathy. *Psychological Bulletin*, *142*(6), 573–600.
- House, T. H., & Milligan, W. L. (1976). Autonomic responses to modeled distress in prison psychopaths. *Journal of personality and social psychology*, *34*(4), 556–560. https://doi.org/10.1037//0022-3514.34.4.556
- Joëls, M., & Baram, T. Z. (2009). The neuro-symphony of stress. Nature Reviews. Neuroscience, 10(6), 459–466. https://doi.org/10.1038/nrn2632
- Johnson, M. M., Mikolajewski, A., Shirtcliff, E. A., Eckel, L. A., & Taylor, J. (2015). The association between affective psychopathic traits, time incarcerated, and cortisol response to psychosocial stress. *Hormones and Behavior*, 72, 20–27. https://doi.org/10.1016/j.yhbeh.2015.04.010
- Lidberg, L., Levander, S., Schalling, D., & Lidberg, Y. (1978). Urinary catecholamines, stress, and psychopathy: A study of arrested men awaiting trial. *Psychosomatic Medicine*, 40(2), 116–125. https://doi.org/10.1097/00006842-197803000-00004
- Loney, B. R., Butler, M. A., Lima, E. N., Counts, C. A., & Eckel, L. A. (2006). The relation between salivary cortisol, callous-unemotional traits, and conduct problems in an

adolescent non-referred sample. *Journal of Child Psychology and Psychiatry*, 47(1), 30–36. https://doi.org/10.1111/j.1469-7610.2005.01444.x

- Lorber, M. F. (2004). Psychophysiology of aggression, psychopathy, and conduct problems: A meta-analysis. *Psychological Bulletin*, *130*(4), 531–552. https://doi.org/10.1037/0033-2909.130.4.531
- Lykken, D. T. (1957). A study of anxiety in the sociopathic personality. *Journal of Abnormal and Social Psychology*, 55(1), 6–10. https://doi.org/10.1037/h0047232
- Meng, X., Rosenthal, R., & Rubin, D. B. (1992). Comparing correlated correlation coefficients. *Psychological Bulletin*, 111(1), 172–175. https://doi.org/10.1037/0033-2909.111.1.172
- Mitchell, D. G. V., Colledge, E., Leonard, A., & Blair, R. J. R. (2002). Risky decisions and response reversal: Is there evidence of orbitofrontal cortex dysfunction in psychopathic individuals? *Neuropsychologia*, 40(12), 2013–2022. https://doi.org/10.1016/S0028-3932(02)00056-8
- Morris, B. H., & Rottenberg, J. (2015). Heightened reward learning under stress in generalized anxiety disorder: A predictor of depression resistance? *Journal of Abnormal Psychology*, 124(1), 115–127. https://doi.org/10.1037/a0036934
- Neumann, C. S., & Hare, R. D. (2008). Psychopathic traits in a large community sample: Links to violence, alcohol use, and intelligence. *Journal of Consulting and Clinical Psychology*, 76(5), 893–899. https://doi.org/10.1037/0022-006X.76.5.893
- Newman, J. P. (1998). Psychopathic Behavior: An Information Processing Perspective. Em D. J.
 Cooke, A. E. Forth, & R. D. Hare (Eds.), *Psychopathy: Theory, Research and Implications for Society* (pp. 81–104). Springer. https://doi.org/10.1007/978-94-011-3965-6_5
- Newman, J. P., & Baskin-Sommers, A. R. (2012). Early selective attention abnormalities in psychopathy: Implications for self-regulation. In *Cognitive neuroscience of attention* (2nd ed., pp. 421–440). Guilford Press.
- Newman, J. P., Curtin, J. J., Bertsch, J. D., & Baskin-Sommers, A. R. (2010). Attention moderates the fearlessness of psychopathic offenders. *Biological Psychiatry*, 67(1), 66–70. https://doi.org/10.1016/j.biopsych.2009.07.035
- Newman, J. P., & Kosson, D. S. (1986). Passive avoidance learning in psychopathic and nonpsychopathic offenders. *Journal of Abnormal Psychology*, 95(3), 252–256. https://doi.org/10.1037/0021-843X.95.3.252

- Newman, J. P., & Schmitt, W. A. (1998). Passive avoidance in psychopathic offenders: A replication and extension. *Journal of Abnormal Psychology*, *107*(3), 527–532. https://doi.org/10.1037//0021-843x.107.3.527
- Oba, T., Katahira, K., & Ohira, H. (2019). The effect of reduced learning ability on avoidance in psychopathy: A computational approach. *Frontiers in Psychology*, *10*(2432), 1–15. https://doi.org/10.3389/fpsyg.2019.02432
- Ossewaarde, L., Hermans, E. J., van Wingen, G. A., Kooijman, S. C., Johansson, I.-M.,
 Bäckström, T., & Fernández, G. (2010). Neural mechanisms underlying changes in stresssensitivity across the menstrual cycle. *Psychoneuroendocrinology*, *35*(1), 47–55. https://doi.org/10.1016/j.psyneuen.2009.08.011
- Paret, C., & Bublatzky, F. (2020). Threat rapidly disrupts reward reversal learning. *Behaviour Research and Therapy*, *131*, 103636. https://doi.org/10.1016/j.brat.2020.103636
- Paternoster, R., Brame, R., Mazerolle, P., & Piquero, A. (1998). Using the correct statistical test for the equality of regression coefficients. *Criminology*, *36*(4), 859–866. https://doi.org/10.1111/j.1745-9125.1998.tb01268.x
- Paulhus, D. L., Neumann, C. S., & Hare, R. D. (2016). *The SRP-4: Self-report psychopaty scale* (4.^a ed.). Multi-Health Systems.
- Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J., & Frith, C. D. (2006). Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. *Nature*, 442(7106), 1042–1045. https://doi.org/10.1038/nature05051
- Petzold, A., Plessow, F., Goschke, T., & Kirschbaum, C. (2010). Stress reduces use of negative feedback in a feedback-based learning task. *Behavioral Neuroscience*, 124(2), 248–255. https://doi.org/10.1037/a0018930
- Porcelli, A. J., & Delgado, M. R. (2017). Stress and decision making: Effects on valuation, learning, and risk-taking. *Current Opinion in Behavioral Sciences*, *14*, 33–39. https://doi.org/10.1016/j.cobeha.2016.11.015
- Pruessner, J. C., Champagne, F., Meaney, M. J., & Dagher, A. (2004). Dopamine release in response to a psychological stress in humans and its relationship to early life maternal care: A positron emission tomography study using [11C]raclopride. *The Journal of Neuroscience*, *24*(11), 2825–2831. https://doi.org/10.1523/JNEUROSCI.3422-03.2004

- Pujara, M., Motzkin, J. C., Newman, J. P., Kiehl, K. A., & Koenigs, M. (2014). Neural correlates of reward and loss sensitivity in psychopathy. *Social Cognitive and Affective Neuroscience*, 9(6), 794–801. https://doi.org/10.1093/scan/nst054
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
- Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, 275(5306), 1593–1599. https://doi.org/10.1126/science.275.5306.1593
- Seara-Cardoso, A., Queirós, A., Fernandes, E., Coutinho, J., & Neumann, C. (2020). Psychometric properties and construct validity of the short version of the Self-Report Psychopathy Scale in a southern European sample. *Journal of Personality Assessment*, *102*(4), 457–468. https://doi.org/10.1080/00223891.2019.1617297
- Seara-Cardoso, A., & Viding, E. (2015). Functional neuroscience of psychopathic personality in adults. *Journal of Personality*, 83(6), 723–737. https://doi.org/10.1111/jopy.12113
- Smith, S. F., & Lilienfeld, S. O. (2015). The response modulation hypothesis of psychopathy: A meta-analytic and narrative analysis. *Psychological Bulletin*, *141*(6), 1145–1177. https://doi.org/10.1037/bul0000024
- Sutton, R., & Barto, A. (1998). Reinforcement Learning: An Introduction. MIT Press.
- Thompson, D. F., Ramos, C. L., & Willett, J. K. (2014). Psychopathy: Clinical features, developmental basis and therapeutic challenges. *Journal of Clinical Pharmacy and Therapeutics*, 39(5), 485–495. https://doi.org/10.1111/jcpt.12182
- Viding, E., McCrory, E., & Seara-Cardoso, A. (2014). Psychopathy. *Current Biology*, 24(18), R871–R874. https://doi.org/10.1016/j.cub.2014.06.055
- Von Borries, A. K. L., Brazil, I. A., Bulten, B. H., Buitelaar, J. K., Verkes, R. J., & De Bruijn, E.
 R. A. (2010). Neural correlates of error-related learning deficits in individuals with psychopathy. *Psychological Medicine*, 40(9), 1559–1568. https://doi.org/10.1017/S0033291709992017
- White, S. F., Pope, K., Sinclair, S., Fowler, K. A., Brislin, S. J., Williams, W. C., Pine, D. S., & Blair, R. J. R. (2013). Disrupted expected value and prediction error signaling in youths with disruptive behavior disorders during a passive avoidance task. *American Journal of Psychiatry*, *170*(3), 315–323. https://doi.org/10.1176/appi.ajp.2012.12060840

Yildirim, B. O., & Derksen, J. J. L. (2015). Mesocorticolimbic dopamine functioning in primary psychopathy: A source of within-group heterogeneity. *Psychiatry Research*, 229(3), 633–677. https://doi.org/10.1016/j.psychres.2015.07.005