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Self-centered or other-directed: Neural correlates of performance monitoring are dependent on psychopathic traits and social context

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ABSTRACT

Performing in a social context can result in negative feelings when our actions harm another person, but it can also lead to positive feelings when observing an opponent fail. The extent to which individuals scoring high on psychopathic traits, often characterized as self-centered with reduced concern for others' welfare, are sensitive to own and others' success and failure is yet unknown. However, knowledge about these processes is crucial for comprehending how these traits are involved in understanding ourselves and others during social interactions. In this functional magnetic resonance imaging (fMRI) study, healthy females scoring low or high on psychopathic traits performed a cannon-shooting game in non-social, cooperative, and competitive contexts. We hypothesized group differences regarding: (1) monitoring of own actions in a non-social context (errors that only negatively affect oneself) versus cooperative context (errors that also harm others), (2) successfully performing with either positive (shared gain) or negative consequences (selfish gain) for the co-player, and (3) observing other's performance leading to shared or selfish gain for oneself. Decreased performance-monitoring-related activations were found in posterior medial frontal cortex for females scoring high on psychopathic traits in the social versus non-social context. When observing others, striatal activations were stronger for selfish gains for high scorers and for shared gains for low scorers. The current outcomes demonstrate that performance-monitoring and reward-related brain activations importantly depend on the interplay between psychopathic traits and social context. We propose that these neural mechanisms may underlie the more self-centered behavior of individuals scoring high on psychopathic traits. As such, the current findings may open up new research avenues, which could advance our understanding of how personality traits impact performance monitoring in a wide variety of social contexts and could possibly lead to the development of interventions aimed at normalizing reduced concern for others.

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1.   Introduction

When performing in a non-social context, people only have to deal with their own failures and the associated negative outcomes. Performing in a social context, however, is often associated with additional cognitive and affective processes (Cracco, Desmet, & Brass, 2016; De Bruijn, de Lange, von Cramon, & Ullsperger, 2009; De Bruijn & von Rhein, 2012; Koban, Corradi-Dell'Acqua, & Vuilleumier, 2013). Errors made in a social context can, for example, lead to enhanced feelings of guilt and shame when your error has negative consequences for another person (De Bruijn, Jansen, & Overgaauw, 2019; Ruissen, Overgaauw, & De Bruijn, 2018; Yu, Hu, Hu, & Zhou, 2014). However, it can also lead to positive feelings, such as pleasure when observing a competitor making a mistake resulting in personal gain (Molenberghs & Louis, 2018; Ruissen et al., 2018). People's understanding of the impact of one's own actions on others as well as the response to others' success and failure is subject to large individual differences. However, understanding the role of individual differences in these processes is crucial for advancing our knowledge about why some people behave in a more self-centered manner, while others are more focused on other-regarding behavior. This especially holds for individuals who score high on psychopathic traits and who often show altered sensitivity to feel with people. Cleckley (1941) describes psychopaths as individuals who have high intellectual abilities enabling them to manipulate others and to, for example, twist things to their own interest. Additionally, their lack of consideration for others due to reduced levels of empathy (Blair, 2018) makes them less responsive to distress in others (Blair, 2013). Moreover, an important feature of psychopaths is their failure to accept responsibility for own actions by externalizing blame (Häkkänen-Nyholm & Hare, 2009). Especially individuals who show high levels of callous and unemotional traits are characterized by empathy deficits and lacking feelings of guilt and shame (Frick & Viding, 2009). Recently, the so-called "self to other model of empathy" has been proposed that directly connects psychopathic traits such as reduced empathy and a shift towards self-centered rather than other-directed behavior to deficits in understanding others (Bird & Viding, 2014). The authors argue that empathy deficits in this population are the result of diminished affective information processing (involving the anterior insula and anterior cingulate cortex), which is — together with contextual information — an important source of information that helps to understand others. Affective information is a representation of your own affective state, either triggered by the self (e.g., memories) or by the emotions of someone else (i.e., emotional contagion). A lacking ability to share feelings can enhance self-centered behavior, which has been supported by a prior study demonstrating higher levels of schadenfreude (i.e., a pleasure derived from the misfortune of others) in individuals reporting higher levels of psychopathic traits (James, Kavanagh, Jonason, Chonody, & Scrutton, 2014; Paulus et al., 2018; Porter, Bhanwer, Woodworth, & Black, 2014). Although research and descriptions on psychopathic traits initially only concerned (violent) criminal offenders, externalizing blame and lower feelings of guilt and shame for own actions have

also been found to be related to psychopathic traits in a sub-clinical sample, supporting the relevance of studying individual differences in community samples (Prado, Treeby, & Crowe, 2016). The current study aims to investigate the role of individual differences in psychopathic traits in healthy female adults when i) monitoring own actions when making mistakes that only negatively affect oneself (non-social context) versus mistakes that additionally negatively affect others (cooperation context), ii) successfully performing with either positive (shared gain) or negative consequences (selfish gain) for the co-player, and iii) observing other's performance leading to shared or selfish gain for oneself.

Studies on performance monitoring have initially been driven by the discovery of an event-related component using electroencephalography (EEG) (Gehring, Gross, Coles, Meyer, & Donchin, 1993). This so-called error-related negativity (ERN) is an increased negative deflection occurring between 60 and 120 msec after an erroneous response (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring et al., 1993). The ERN is assumed to play a role in our ability to learn from our errors and is followed by a positive component known as the error positivity (Pe), thought to be involved in more conscious, evaluative aspects of error processing (O'Connell et al., 2007; Ullsperger, Danielmeier, & Jocham, 2014). Detecting our errors and learning from them can be achieved through constant monitoring of our performance, and this process thus enables flexible behavior (De Bruijn et al., 2009; Izuma, Saito, & Sadato, 2010). Studies using functional magnetic resonance imaging (fMRI) have shown that performance monitoring heavily relies on posterior medial frontal cortex (pMFC) and bilateral anterior insula (AI) with increased activations for error versus correct responses. pMFC activations typically include anterior midcingulate cortex (aMCC) and pre-supplementary motor area (pre-SMA) (see e.g., Botvinick, Cohen, & Carter, 2004; De Bruijn et al., 2009; Debener et al., 2005; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). In contrast, activation in the striatum is more pronounced for positive compared to negative outcomes (see e.g., De Bruijn et al., 2009).

Initial research on performance monitoring focused on individual, i.e., non-social contexts. However, humans are social creatures, meaning that our actions often have consequences for the people around us and that we need to adapt our behavior in response to others' actions. As a result, researchers have more recently started to focus on social performance monitoring. De Bruijn et al. (2009), for example, investigated the role of the social context in performance monitoring by letting healthy volunteers perform the so-called Cannonball task in which they had to play with (cooperative context) or against (competitive context) an unknown peer. fMRI results showed that pMFC was similarly activated for own and observed errors, irrespective of whether the co-actor was a cooperative partner or an opponent (for a similar finding using EEG see De Bruijn & von Rhein, 2012). The striatum, however, showed distinctive activation depending on the financial outcome; increased activity was found for own and observed correct actions as well as for incorrect actions from an opponent, highlighting its role in reward-related processing. Thus, striatum was activated for shared gains, but also for gains at the expense of another person, so-called

selfish gains. A study by Koban et al. (2013) demonstrated that making harmful mistakes (i.e., mistakes that cause pain in others) resulted in increased activations in AI compared to non-harmful mistakes, highlighting the role of AI in guiding behavior through affective signals.

The aim of the current study is to investigate the neural mechanisms of social performance monitoring in healthy females scoring either low or high on psychopathic traits. So far, only EEG studies have investigated performance monitoring in individuals scoring high on psychopathic traits. However, these studies only investigated non-social contexts and mainly included incarcerated violent offenders with psychopathy. Results demonstrated a pattern of unaffected ERN amplitudes combined with reduced Pe amplitudes in both males (Brazil et al., 2009; Munro et al., 2007) and females (Maurer et al., 2016). Both behavioral and EEG studies have repeatedly demonstrated learning deficits in offenders with psychopathy, specifically for reinforcement learning (Von Borries et al., 2010) and reversal learning (Blair, 2017; Mitchell et al., 2006). To our knowledge, only one EEG study did investigate the role of social context and psychopathy when monitoring performance in a passive observation paradigm (Brazil et al., 2011). Brazil et al. (2011) showed overall reduced electrophysiological responses for both observed correct and incorrect actions in psychopathic individuals, suggestive of diminished overall performance monitoring specifically in social contexts. Nonetheless, the role of individual differences in psychopathic traits in the neural processing of errors and rewards in both non-social and more interactive social contexts have not been investigated in a healthy sample. This is surprising given the social nature of human behavior in general and of psychopathy in particular. Similar to social context, psychopathic traits in females have received much less attention than males in research so far. Investigating females is especially relevant for social performance monitoring research, as females generally show higher levels of empathic abilities – i.e., consideration for the feelings of others – compared to males, making them more sensitive for social evaluations but also better equipped while socially interacting with others (e.g., Christov-Moore et al., 2014). Interestingly, especially when empathy is low in females scoring high on psychopathic traits, this affective personality trait has been found to be a good predictor of future violent behavior (Thomson, Bozgunov, Psederska, & Vassileva, 2019). This effect was absent in males scoring high on psychopathic traits. In males, behavioral psychopathic traits like impulsivity and risk-taking behaviors have been found to be the best predictors of future violence and aggression. Even though this study specifically focused on aggressive behavior, it does indicate that gender plays a role regarding which personality trait "activates" specific behavior in individuals scoring high on psychopathic traits (Thomson et al., 2019).

Additionally, a review study by Whittle, Yücel, Yap, and Allen (2011) demonstrated that males and females activate different neural regions when it comes to the processing of emotions. The current study involves an important social component, because subjects are responsible for the other person's monetary outcome in a cooperative and competitive context, and because observing others' performance lead to own gains and/or losses. Since these social processes could involve emotion processing and feelings of empathy, which has been found to be especially of influence in females (Thomson et al., 2019), we decided to only include females. In addition, several prior studies demonstrated significantly higher psychopathic trait scores in males versus females in community samples (Berkhout, Young, & Gross, 2011; Cale & Lilienfeld, 2002; Hemphälä & Tengström, 2010). We decided to specifically focus on the underrepresented female sample in order to rule out the possibility of only including high scoring male participants. This is of specific importance as we pre-selected individuals from a large existing database representing the 25% scoring highest and the 25% scoring lowest on self-reported psychopathic traits (in line with Shao & Lee, 2017). Based on the marked self-centeredness and reduced concern for others in individuals who score high on psychopathic traits, we expected to find decreased error-related activations in pMFC and AI compared to individuals scoring low on psychopathic traits; specifically for mistakes that negatively affect both oneself and another person. Moreover, we expected to find enhanced reward-related activations in striatum for selfish compared to shared gains, while the reverse was expected for low scoring participants.

2. Methods

2.1. Participants

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. In this study, a total of 49 healthy right handed females aged between 18 and 31 participated. We pre-selected females representing the lower and upper quartiles of a female distribution on the validated Dutch translation of the short-form of the psychopathic personality inventory-short form (PPI-SF: Tonnaer, Cima, Sijtsma, Uzieblo, & Lilienfeld, 2013; see Questionnaires). See Table 1 for an overview of the group characteristics, and for group differences based on independent sample t-tests. This selection was done based on the self-reports of 1057 female Psychology and Educational Science students who completed an online survey study advertised on the Leiden University Research Participation System (SONA). Exclusion criteria were: current or previous medical or psychiatric disorders, and use of medication that could influence cognitive functioning. As a result of technical problems with the scanner, we excluded 3 participants. Additionally, due to excessive movement on 1 or more runs, we excluded 7 participants. A total of 38 participants (19 females scoring low) were included in the final analyses ($N = 38$, Mean Age = 19.45, SD = 2.01). Participants completed the experiment for course credits or monetary compensation and provided written informed consent. In case participants completed the experiment for course credits, they received their earned bonus in cash. The bonus they received was not actually based on their performance on the task but randomly selected between 0 and €15 euros. The Institutional Review Board of the Leiden University Medical Center approved all procedures. The current

Table 1 – Group characteristics of females scoring low or high on psychopathic traits (means and standard deviations).

	Low PPI (N = 19)	High PPI (N = 19)	Group differences p-value
Age	19.42 (1.43)	19.47 (2.50)	.937
PPI-SF total	170.27 (5.25)	231.37 (7.94)	<.001
F1 (Fearless Dominance) total	71.73 (12.32)	93.62 (16.25)	= .004
F2 (Self-centered Impulsivity) total	81.45 (9.47)	119.37 (8.77)	<.001
Machiavellian Egocentricity	26.18 (5.25)	38.87 (4.85)	<.001
Social Potency	35.45 (7.41)	45.12 (9.54)	= .023
Fearlessness	22.55 (6.93)	32.00 (4.72)	= .004
Coldheartedness	17.09 (3.45)	18.37 (3.42)	.432
Impulsive Nonconformity	17.91 (2.91)	27.62 (4.53)	<.001
Externalization of Guilt	14.91 (3.48)	23.62 (5.90)	= .001
Carefree Nonplanfulness	22.45 (4.76)	29.25 (6.02)	= .014
Stress Immunity	13.73 (2.94)	16.50 (5.32)	.211

study was conducted in accordance with the Declaration of Helsinki.

2.2. Experimental task and procedure

Participants performed the validated Cannonball task, which has been used before in studies investigating social performance monitoring processes (De Bruijn et al., 2009; Radke, de Lange, Ullsperger, & de Bruijn, 2011). The aim was to stop a horizontally moving cannon (two-dimensional triangle-shaped figure) by precisely lining it up with the stationary 2-dimensional square target by a button press (see Fig. 1). Hitting the target resulted in a monetary gain (€0.10), and missing the target resulted in a monetary loss (€0.10).

Three same-sex participants were invited to the scanner to participate in a joint shooting game of which one participant would go into the scanner, while the other two players would play from separate rooms. They were explained that they would play the game – consisting of the following 3 blocks: an individual block, a cooperative block, and a competitive block – online. During the introduction phase, the three participants had to practice the task together in the same room. Prior to the scanning session, two out of three participants were directed to separate rooms where they were explained that they would not actually perform the Cannonball task but another unrelated behavioral task. After they finished the task, they received course credits or monetary compensation for their participation.

Thus, the participant in the scanner did not actually play with and against the two unknown peers. In reality, the computer mimicked actual performance of the participant with a delay to balance own performance and performance of the co-actors throughout the experiment. The blocks were counterbalanced between participants, and the experimenter verbally explained whom they would cooperate with and whom they would compete against before the task started and in between blocks.

In line with previous studies using this paradigm (De Bruijn et al., 2009; Radke et al., 2011), the size of the target was dynamically adapted based on the participants' performance such that a mean hit rate of around 63% was achieved. This was done in order to reach the same level of errors and correct trials in each individual, which enabled us to make contrasts based on a comparable number of trials across groups and contexts. Note that the use of an adaptive criterion thus ensured that performance is controlled for in the Cannonball task, such that behavioral effects are not expected nor of interest in this study. The change in target size was determined after each trial by comparing the current actual percentage of correct trials and the goal percentage of correct trials using the following formula: Change=(Actual_Percentage_Correct−Goal_Percentage_Correct)*Change_Factor)/100*Current_Target_Size). The Change_Factor was set at .25 based on previous studies using the same paradigm (see De Bruijn et al., 2009; Radke et al., 2011). When the current percentage was higher than the goal percentage, the change was subtracted from the current target size. When the current percentage was lower than the goal percentage, the change was added. This dynamic procedure was newly applied at the start of each context and thus ensured that the 63% percent hit rate was achieved independently for each context.

The task was played in three different contexts: individual (non-social), cooperation (social; co-actor 1), and competition (social; co-actor 2). In the individual context, the participant played 80 trials alone (8 blocks of 10 trials). Hitting or missing the target only affected their own monetary outcome (see Fig. 2). In the cooperative and competitive context, participants alternated between performing and observing in 16 blocks of 10 trials each (8 blocks playing, 8 blocks observing). In both cases, the performance of the person playing had a direct effect on the financial outcome of the co-actor. For the cooperative context, stopping the cannon under the target resulted in a shared monetary gain (plus €0.10 each), and missing the target resulted in a shared monetary loss (minus €0.10 each). For the competitive context, hitting the target resulted in a monetary gain for the player (plus €0.10), but in a monetary loss for the co-actor (minus €0.10). Missing the target on the other hand resulted in a monetary loss for the player (minus €0.10), but in a monetary gain for the co-actor (plus €0.10).

Prior to the presentation of each stimulus, a jittered fixation cross appeared between 750 and 1250 msec. Target location was randomly determined on each trial, whereas the cannon was always horizontally centered. Immediately after presentation, the cannon started moving either to the right or the left for a maximum of 2.5 lengths (3500 msec) in total. An unambiguous feedback signal (thumbs up/thumbs down) was presented 750 msec after the button press, indicating whether the response resulted in a hit or a miss. Each block started with a cue instructing participants about whether they were playing in the individual, cooperative, or competitive context. Additionally, the words "you play" or "you observe" were presented in the center of the screen to indicate what was expected of participants.
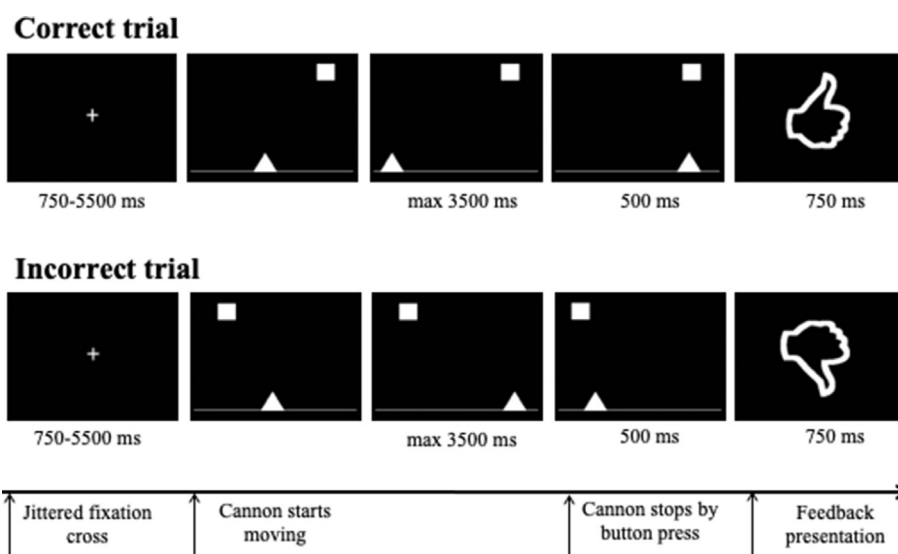
Fig. 1 — Example of a Correct and an Incorrect trial. The aim of the task is to stop a horizontally moving cannon (triangle) by a button press, precisely lining it up with a stationary target to shoot the target (square). A mini-block design was used in which participants alternate between performing and observing in blocks of 10 trials each. The size of the target was dynamically adapted based on the participants' performance such that a mean hit rate of 63% would be achieved. Participants win 10 cents for hitting the target and lose 10 cents for missing the target.

2.3. Questionnaires

To assess psychopathic traits, participants completed the Dutch translation of the PPI-SF (Tonnaer et al., 2013). The 100-item PPI-SF is answered on a 4-point Likert scale (1-*false* and 4-*true*) and contains 8 subscales: 1. Machiavellian Egocentricity (ruthlessness and narcissism in interpersonal functioning), 2. Social Potency (perceived ability to influence and manipulate others), 3. Coldheartedness (callousness, guiltlessness, and unsentimentality), 4. Carefree Nonplanfulness (attitude of indifference in planning one's actions), 5. Fearlessness (absence of anticipatory anxiety concerning harm and risk taking behavior), 6. Blame Externalization (externalizing and rationalizing misbehavior), 7. Impulsive Nonconformity (reckless lack of concern regarding social mores), and 8. Stress Immunity (absence of emotional reactions to anxiety-

	PLAY		OBSERVE	
SOLO	+ € .10	- € .10	n.a.	n.a.
COOPERATION	+ € .10	- € .10	+ € .10	- € .10
COMPETITION	+ € .10	- € .10	- € .10	+ € .10

Fig. 2 — Reward outcomes when playing alone (non-social context) or when playing with a co-actor in a cooperative or competitive situation (social context). In the social contexts, the participant and the co-actor interchangeably play and observe.

provoking events). The PPI-SF can be subdivided in two higher-order factors: F1) Fearless Dominance, consisting of the subscales Social Potency, Fearlessness, and Stress Immunity, and F2) Self-centered Impulsivity, consisting of the subscales Machiavellian Egocentricity, Carefree Nonplanfulness, Blame Externalization, and Impulsive Nonconformity.

2.4. fMRI data analysis

MRI scans were obtained with a Philips 3.0 T MRI scanner at the Leiden University Medical Center. Foam inserts that surrounded the head restricted head motion. Functional scans for the task were acquired during three runs with T2-weighted echo-planar imaging (EPI). The first two volumes of each run were discarded to allow for equilibration of T1 saturation effects. After the functional scanning the following settings were used: TR = 2.2 sec, TE = 30 msec, sequential acquisition, 38 slices, slice thickness = 2.75 mm, Field of View (FOV) = 220 × 220 × 114.68 mm.

The experimental task was projected on a screen, which was visible to participants through a mirror. Data were analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London). The following pre-processing steps were used: correction for slice timing acquisition and rigid body motion, spatial normalization to T1 templates (MNI305 stereotaxic space) using a 12-parameter affine transform together with a nonlinear transformation involving cosine basis functions and resampling of the volumes to 3 mm voxels. Functional scans were smoothed with an 8 mm FWHM isotropic Gaussian kernel. The 38 participants who were included in the final analyses had a mean maximum head movement of .93 and an absolute maximum head movement of 3.16 mm.

All events were time locked to the onset of the outcome screen. The trial functions were used as covariates in a general linear model; along with a basic set of cosine functions that high-pass filtered the data. The least-squares parameter estimates of height of the best fitting canonical HRF for each context were used in pair-wise contrasts. The resulting contrast images, computed on a subject-by-subject basis, were submitted to group analyses. We tested the neural response to feedback (thumbs up: hit, thumbs down: miss) with two full factorial designs in line with prior studies using the Cannonball task (De Bruijn et al., 2009; Radke et al., 2011).

To identify the areas typically involved in performance monitoring and reward processing, based on prior studies by De Bruijn et al. (2009) and Radke et al. (2011), full factorial designs were computed. First, we tested for the main effect of Error > Correct by performing a 2 (Context: Individual, Cooperation) × 2 (Correctness: Correct, Error) × 2 (Group: PPI low, PPI high) full factorial design. Second, the main effect of Gain > Loss was computed using a 2 (Context: Cooperation, Competition) × 2 (Agency: Play, Observe) × 2 (Outcome: Gain, Loss) × 2 (Group: PPI low, PPI high) full factorial design. Main effects were considered significant if they exceeded a family-wise error (FWE) voxel level threshold of $p < .05$.

Next, we performed anatomical region of interest (ROI) analyses using the Marsbar toolbox in SPM8 (Brett, Anton, Valabregue, & Poline, 2002) for the AI and striatum in order to further investigate patterns of activation for error and reward mechanisms. These anatomical regions have been selected based on previous studies (De Bruijn et al., 2009; Radke et al., 2011) and were derived from the MarsBaR anatomical toolbox. Additionally, since there is no anatomical pMFC available in the MarsBaR anatomical toolbox, we performed ROI analyses on a 10 mm radius sphere of the pMFC centered on 4, 32, 38 (De Bruijn et al., 2009). Beta values reflecting activity were averaged across all voxels in the cluster, resulting in a mean value per ROI for each condition for each participant.

3. Results

3.1. Behavioral data

As expected from the use of the adaptive criterion, a 3 (Context: Individual, Cooperative, Competitive) × 2 (Group: low PPI, high PPI) repeated-measures ANOVA showed no significant differences in average hit rate, neither for condition [$F(2,72) = 2.88$, $p = .06$], nor for group [$F(1,36) = 2.29$, $p = .14$]. A 2 (Context: Cooperation, Competition) × 2 (Agency: Play, Observe) × 2 (Group, low PPI, high PPI) repeated-measures ANOVA, showed equal average hit rates in both the cooperative and competitive context [$F(1,36) = .16$, $p = .69$], both when playing and observing [$F(1, 36) = .13$, $p = .72$], and both in the low and high PPI group [$F(1,36) = 1.22$, $p = .28$]. For the means, see Table 2.

Next, we ran the same models with the dependent variable Target Size and the additional factor Correctness. These analyses only showed the expected main effects of Correctness (both p's < .001) with larger target sizes for correct (mean) compared to incorrect responses (mean), but none of the main effects of Group, nor interactions with Group reached significance (all F's < 2.68; all p's > .11).

3.2. fMRI analyses

3.2.1. Whole brain contrast: monitoring own actions when making mistakes that only negatively affect oneself (individual, non-social context) versus mistakes that additionally negatively affect others (cooperative context)

3.2.1.1. Main effect Error > Correct (individual & cooperation). The whole brain contrast for Error > Correct revealed more activation in pMFC (6, 20, 43; FWE corrected, $p < .05$), and bilateral AI left AI: −39, 17, −2, right AI: 36, 20, 7; FWE corrected, $p < .05$) in line with the study of the De Bruijn et al. (2009), and Radke et al. (2011) (see Fig. 3A).

3.2.1.2. ROI analyses (play).
3.2.1.2.1. Playing unsuccessfully leading to shared (cooperation) or own (individual) loss. For the pMFC (see Fig. 3), we found no significant main effect for Context or Group, nor did we find a significant interaction for Correctness*Group,

Table 2 — Average hit rates (in %) of females scoring low or high on psychopathic traits (means and standard deviations).

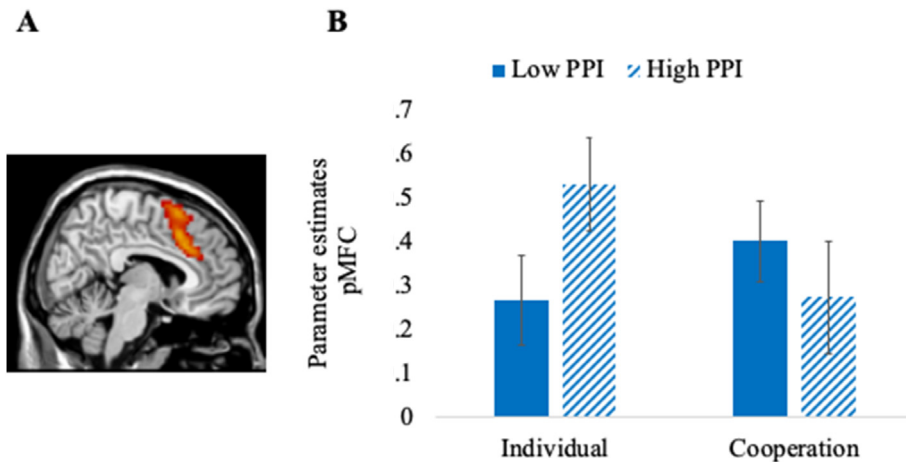|	Play			Observe	
	Individual Mean (SD)	Cooperation Mean (SD)	Competition Mean (SD)	Cooperation Mean (SD)	Competition Mean (SD)
Average hit rate					
Low PPI group	63.3 (1.9)%	64.2 (2.7)%	64.4 (2.0)%	64.7 (5.4)%	63.6 (3.6)%
High PPI group	62.6 (2.1)%	63.1 (2.6)%	63.8 (2.7)%	62.6 (7.1)%	63.7 (4.4)%
Target size					
Low PPI group	24.10 (4.76)	24.27 (6.03)	22.72 (4.33)	24.27 (6.03)	25.70 (5.25)
High PPI group	26.11 (5.61)	25.70 (5.25)	25.77 (6.00)	22.72 (4.33)	25.77 (6.00)

Fig. 3 — A) Whole brain contrast (full factorial design) for the main effect of Error > Correct for N = 38 (FWE corrected, *p* < .05) revealed posterior medial frontal cortex activation. B) Interaction effect for Context*Group based on the parameter estimates of the pMFC. The low PPI group showed no difference in activation between Individual and Cooperation, whereas the high PPI group showed significantly higher activation for the Individual versus the Cooperation Context. Results showed no significant between group effects.

Context*Correctness or Context*Correctness*Group (all *p*'s > .43). However, we did find a significant interaction effect for Context*Group [*F*(1,36) = 6.52, *p* = .02, η^2 = .15] (see Fig. 3B). Follow-up tests *within* group for the pMFC demonstrated that the high scoring group showed significant higher activation for the Individual versus the Cooperative Context (*p* = .02). The low scoring group showed no significant difference between the two contexts (*p* = .15). *Between* group follow-up tests showed no significant effects (all *p*'s > .15).

For the left AI, results showed no significant main effect for Context or Group, nor any significant interactions (all *p*'s > .14). For the right AI, results also showed no significant main effect for Context or Group, nor any significant interaction effects (all *p*'s = .08).

3.2.2. *Whole brain contrast: own rewards in a social context with either positive (shared gain) or negative consequences (selfish gain) for the co-player*
3.2.2.1. MAIN EFFECT: GAIN > LOSS (COOPERATION & COMPETITION). The whole brain contrast for Gain > Loss revealed more activation in bilateral striatum (left striatum: −15, 14, −8; right striatum: 15, 14, −11; FWE corrected, *p* < .05) in line with the study of De Bruijn et al. (2009) (see Fig. 4A).

3.2.2.2. ROI ANALYSES (COOPERATION AND COMPETITION)
3.2.2.2.1. PLAYING SUCCESSFULLY LEADING TO SHARED (COOPERATION) OR SELFISH GAIN (COMPETITION) FOR ONESELF. None of the main effects or interactions for both the left and right striatum were significant (all *p*'s > .14).
3.2.2.2.2. OBSERVING OTHER'S PERFORMANCE LEADING TO SHARED (COOPERATION) OR SELFISH GAIN (COMPETITION) FOR ONESELF. For the left striatum, results showed no significant main effect for Context or Group, nor significant interactions for Context*Group, Correctness*Group, or Context*Correctness (all *p*'s > .11). Results did show a significant interaction effect for Context*Outcome*Group [*F*(1,36) = 4.66, *p* = .04, η^2 = .12] (see Fig. 4B). Follow-up tests *within* group demonstrated that the low PPI group showed enhanced activation for shared gains compared to shared loss during observation (*p* = .03), while the high PPI group showed enhanced activation for selfish gains compared to selfish loss while observing the co-actor (*p* = .01). Additionally, results showed a trend significant *within* group effect for the low PPI group, showing less deactivation when losing money in a competitive context versus a cooperative context (*p* = .08). Next, follow-up tests *between* group showed a significant difference for losses in the cooperative context. The high scoring group showed significant
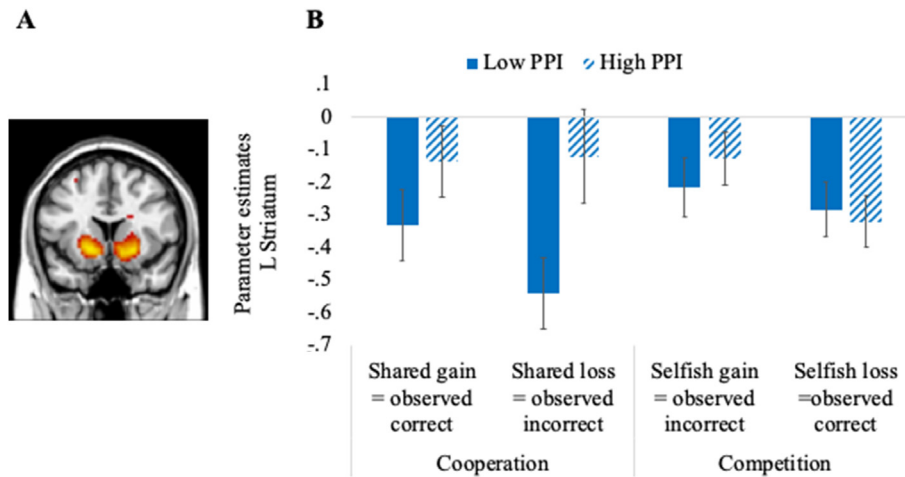
Fig. 4 — A) Whole brain contrast (full factorial design) for the main effect of Gain > Loss for N = 38 (FWE corrected, p < .05). B) Significant interaction effect for Context*Outcome*Group for Observe in the left striatum. Within groups, results showed the following: the low PPI group showed enhanced activation for shared gains compared to shared loss during observation, while the high PPI group showed enhanced activation for selfish gains compared to selfish loss while observing the co-actor. This effect was only significant for Observe, not for Play.

more striatal activation compared to the low scoring group (p = .03).

For the right striatum, results showed no significant main effect for Context, nor any significant interaction for Context*Group, Correctness*Group, or Context*Correctness (all p's > .10). We only found a trend significant main effect for group [$F_{(1,36)}$ = 4.09, p = .05, η^2 = .10], and a trend significant interaction effect for Context*Correctness*Group [$F_{(1,36)}$ = 3.54, p = .07, η^2 = .09].

4. Discussion

Our aim was to improve our understanding of the role of individual differences in psychopathic traits in social performance monitoring. First, the results showed the expected involvement of pMFC for incorrect versus correct actions, as well as striatum for shared and selfish rewards. Second, females scoring high on psychopathic traits showed decreased activation in pMFC when monitoring own actions while performing in a cooperative context in which actions additionally affected their co-player versus performing in an individual context in which actions only affected themselves. Third, the low PPI group showed increased striatal activity specifically when observing co-actors' performance leading to shared gains, whereas the high PPI group only showed this pattern for observing performance resulting in selfish gains.

Involvement of pMFC and AI in performance monitoring has been demonstrated repeatedly in non-social contexts (see e.g., Botvinick et al., 2004; Ridderinkhof et al., 2004) with stronger activations reflecting enhanced monitoring. More recently, these areas have also been highlighted in fMRI studies on performance monitoring in a social context (Cracco et al., 2016; De Bruijn et al., 2009; Koban et al., 2013) as well as in EEG studies that mainly focused on social modulations of

the ERN (see e.g., Brazil et al., 2011; De Bruijn, Ruissen, & Radke, 2017; De Bruijn & von Rhein, 2012; Koban, Pourtois, Bediou, & Vuilleumier, 2012; Koban, Pourtois, Vocat, & Vuilleumier, 2010). This work has amongst others shown that — in healthy adults — performance monitoring is enhanced when participants' actions have consequences for others. Performance monitoring was, for example, increased in cooperative situations, thought to reflect increased motivation to perform well in order to prevent feelings of guilt or shame when playing for a team (Koban et al., 2012). The results from this EEG study additionally showed that this motivation was specifically elevated for individuals reporting high levels of perspective taking, highlighting individual differences. Moreover, a recent study from our lab showed that performing in a social context with potentially harmful (loud aversive sound) versus non-harmful (soft non-aversive sound) consequences for another person led to amplified early performance monitoring processes (enhanced ERN amplitudes), increased levels of arousal, and enhanced effort to perform well (De Bruijn et al., 2019). Finally, another study from our lab revealed larger ERN amplitudes after oxytocin administration, but only for mistakes that additionally negatively affected a co-actor's chance of winning extra money (De Bruijn et al., 2017). This finding suggests that oxytocin levels may specifically modulate error significance in a social context, emphasizing again the role of individual differences in this process.

Although the overall analyses showed the expected pattern of concurrent activation of pMFC and AI for erroneous compared to correct actions, group effects were restricted to the pMFC. For the pMFC, the high PPI group showed decreased activation for cooperative versus individual contexts independent of correctness. This effect was absent for the low PPI group. pMFC is thought to play a central role in performance monitoring and action control, activated amongst others by

(dopamine-driven) proprioceptive prediction errors that facilitate behavioral adjustment (Ullsperger et al., 2014). The AI, however, has been shown to be specifically involved in interoception and error awareness (see e.g., Hester, Foxe, Molholm, Shpaner, & Garavan, 2005; Klein, Ullsperger, & Danielmeier, 2013) emphasizing its affective role in performance monitoring and guiding behavioral adjustments (see also Koban et al., 2013). The high scorers in the present study displayed enhanced performance monitoring in pMFC when consequences of their actions only affected themselves, suggesting that they experienced enhanced error significance in this context facilitating performance monitoring and leading to a stronger tendency to, for example, prevent errors or adjust their behavior adequately. This effect was absent for the low PPI group. The outcome of reduced pMFC activation for the cooperative context in the high PPI group may be explained by a study performed by Klucharev, Munneke, Smidts, and Fernández (2011), who showed that suppressing the pMFC by transcranial magnetic stimulation led to lower levels of adaptive behavior after experiencing a social conflict. Possibly, psychopathic traits are related to a default downregulation of this area when monitoring performance in social situations. This interpretation fits with the EEG findings from Brazil et al. (2011) who showed reduced performance monitoring in incarcerated individuals with psychopathy, but only when observing others' actions and not when performing themselves. This possible default downregulation of the pMFC when performing in a cooperative context may be due to the fact that individuals scoring high on psychopathic traits do not experience errors made in a social context — including the additional social threat of being evaluated — as more aversive compared to an individual context (Rilling et al., 2007). This might suggest distorted emotional saliency (Seara-Cardoso, Sebastian, Viding, & Roiser, 2015), which may result in differences in general motivation and/or cognitive efforts to monitor performance in a social context.

Contrary to our expectations, performance monitoring was not enhanced in a social context in AI. We had expected AI involvement, because previous studies had demonstrated AI activations related to increased error significance and/or associated distress of the possibility of making mistakes that negatively affect others (Koban et al., 2013; Seara-Cardoso, Sebastian, et al., 2015). Koban et al. (2013) for example showed that AI was specifically involved when making harmful mistakes and proposed that AI generates an affective signal that may guide subsequent adjustment. Additionally, Cracco et al. (2016) conducted a study in which AI was activated when observing a co-actor make a mistake for which the participant was partly responsible. Moreover, they found that AI activation was directly related to self-reported feelings of guilt and responsibility. Next, although we found an overall effect of increased AI activation for erroneous versus correct trials, we did not find any significant group differences in this brain area. We expected group differences in AI activations based on a study that focused on the role of individual differences in psychopathic traits when being responsible for other people's pain by delivering electroshocks (Molenberghs et al., 2014). Results revealed an association between psychopathy scores and (left) AI when punishing another person for giving an incorrect answer. These results were explained by a lack of

empathy and fit with previous neuroimaging studies that showed deficits in high scorers in empathic responding toward others in distress (Blair, Mitchell, & Blair, 2005; Decety, Skelly, & Kiehl, 2013; Seara-Cardoso, Viding, Lickley, & Sebastian, 2015). Although the current data suggest that individuals scoring high on psychopathic traits do not seem to have specific deficits in generating such affective signals in situations where one's actions affect others, we did see a trend showing higher AI activity for low scorers during errors. One explanation may be that our currently used monetary consequences — compared to pain stimuli often used in previous studies (Koban et al., 2013; Yu et al., 2014) — were simply not strong enough to evoke clear affective effects of these individual differences. Future studies should further investigate the role of AI in relation to psychopathic traits when levels of responsibility and action consequences differ. Taken together, the current results showed decreased activation in pMFC in cooperative versus individual contexts for the high PPI group, which is in line with their reduced concern for how their actions may affect others and their overall goal-directed egocentric behavioral style aimed at personal gain (see S1).

Next, our findings demonstrated differences in striatal activity for observing performance resulting in shared or selfish monetary gain. Although striatal activity may represent other processes such as motivation or decision-making, the results do fit with the well-established role of striatum in reward processing (see e.g., Delgado, 2007). The current pattern of outcomes thus suggests that low scoring individuals experience shared gains as more rewarding than selfish gains, while the high scorers show the reversed pattern. The enhanced striatal activity in the high scoring group when observing their co-actor fail — resulting in personal gain — may in part be explained by the concept of "schadenfreude", a pleasure derived from the misfortune of others (Dvash & Shamay-Tsoory, 2011; Porter et al., 2014). Takahashi et al. (2009) showed a positive relationship between self-reported schadenfreude and striatal activity when an unfortunate event happened to an envied person. Although fMRI studies in this population are lacking, behavioral studies have demonstrated a positive relationship between psychopathic personality traits and self-reported schadenfreude (James et al., 2014; Paulus et al., 2018; Porter et al., 2014). The competitive context may even have strengthened the schadenfreude experience for the high scorers (Abell & Brewer, 2017, while in the low scorers this context may have enhanced feelings of empathy towards the co-actor (see S1, Lamm, Decety, & Singer, 2011). Paulus et al. (2018) describe feelings of empathy when noticing or hearing about another person's misfortune as "fremdscham", which can be explained as an affective state derived from the emotional state of the person you empathize with (Bird & Viding, 2014). However, more research is needed to understand what exactly is driving the currently found group differences.

One limitation of the current study is that we used a rather arbitrary cut-off point to classify participants into the low or high scoring group. However, it should be noted that the PPI-SF does not define cutoffs to delineate a clinical and/or subclinical range. Therefore, we pre-selected individuals from a large existing database representing the top 25% and bottom 25% of self-reported psychopathic traits creating two groups

representing the opposite ends of the distribution. Another limitation is the relatively small sample size. To overcome these issues, future studies may additionally aim at employing a dimensional approach using a larger sample enabling a focus on the full range of psychopathic trait levels. Moreover, since we believe that feelings of responsibility play a role in the extent to which making a mistake in a social context affects performance-monitoring behavior, it would be interesting to assess self-reported levels of responsibility, schadenfreude, and fremdscham regarding making mistakes in a social context. Finally, we like to point out that the brain areas we currently found to be activated have also been implicated in signaling prediction errors, i.e., the discrepancy between expected and actual outcomes (Brown & Braver, 2005; Knutson & Cooper, 2005; Pagnoni, Zink, Montague, & Berns, 2002). These expectancies can be objective or subjective and the social context may have an impact on the latter. A recent study from our lab, for example, demonstrated that making mistakes in a context where participants were more motivated to perform well resulted in larger error-related negativities (ERN), an ERP component thought to reflect prediction errors. This increase was present in the absence of actual performance differences that could drive objective expectancy violations (see De Bruijn et al., 2019). In the current study, however, it is not so straightforward to explain the current results in terms of prediction errors. First of all, objective expectancy violations cannot, for example, explain the pattern of striatal activation currently found. As performance was kept under control, all conditions resulted in the occurrence of positive feedback signals in 63% and negative feedback signals in 37% of all trials. Negative feedback signals (or incorrect responses) were thus less frequent and should be more unexpected. However, striatum mainly responded to the personal monetary consequence of the feedback (gain or loss) with decreased activations for losses also present in the competitive context. One could argue though that the activation patterns in the competitive context might reflect subjective expectancy violations to a certain extent. For example, high scoring individuals might expect to beat their opponents and thus observe them fail. Observing their opponent perform correctly would then thus be associated with a bigger loss than expected. However, because we did not measure the (subjective) expectancies in our task we cannot draw any conclusions regarding the role of prediction errors in the current outcomes. Future studies should therefore focus on including additional subjective measures on expectancies in order to get a better insight in what is driving differences in brain activity.

The current study also opens up new research avenues. For example, because of the close link between reward sensitivity and learning (Berridge, 2000), it would be interesting to investigate whether healthy individuals scoring high on psychopathic traits also rely on distinct neural mechanisms during reward-dependent learning in a social context. Would performance for example be different when learning in a cooperative versus competitive context? Previously reported observations for example showed that non-criminal individuals scoring high on psychopathic traits seem to thrive especially well in highly competitive work settings (Babiak & Hare, 2006; Ten Brinke, Black, Porter, & Carney, 2015). Thus,

our findings not only reveal the neural mechanisms underlying individual differences in the level of concern for others (see S2) during social performance monitoring, but they may also have important implications for educational and perhaps even clinical and treatment settings. Although we are not able to translate these findings to incarcerated populations, it would be interesting to investigate the role of social context in learning from mistakes, as this may form a starting point for developing interventions aimed at normalizing reduced concern for others.

5.   Conclusions

Using a validated social performance monitoring paradigm, the current study provides evidence for distinct activation patterns in pMFC in healthy non-incarcerated females scoring low or high on psychopathic traits when monitoring performance in situations in which the level of responsibility for others varies. Moreover, when another person is responsible for your benefits, sharing gains is associated with less or more reward-related activation in striatum compared to selfish gains depending on the level of psychopathic traits. The present findings thus demonstrate for the first time that performance monitoring and reward-related processes in different social contexts are dependent on psychopathic traits in healthy females. We propose that these altered processes may play a role in the known shift from other-directed to self-centered behavior in individuals with psychopathy and may hence partly explain the deficits these individuals have in understanding others (cf. Bird & Viding, 2014).

Competing financial interests

None of the authors reported competing financial interests or potential conflicts of interest.

Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the study are available at https://dataverse.nl/dataset.xhtml?persistentId=hdl:10411/0S1YPP.

Pre-registration

No part of the study procedures reported within this manuscript was pre-registered prior to the research being conducted.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2020.01.030.

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