



Sex differences in the neural underpinnings of social and monetary incentive processing during adolescence

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Published online: 13 February 2018
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Abstract

The brain's reward system undergoes major changes during adolescence, and an increased reactivity to social and nonsocial incentives has been described as a typical feature during this transitional period. Little is known whether there are sex differences in the brain's responsiveness to social or monetary incentives during adolescence. The aim of this event-related potential (ERP) study was to compare the neurophysiological underpinnings of monetary and social incentive processing in adolescent boys versus girls. During ERP recording, 38 adolescents (21 females, 17 males; 13–18 years) completed an incentive delay task comprising (a) a reward versus punishment condition and (b) social versus monetary incentives. The stimulus-preceding negativity (SPN) was recorded during anticipation of reward and punishment, and the feedback P3 (fP3) along with the feedback-related negativity (FRN) after reward/punishment delivery. During anticipation of social punishment, adolescent boys compared with girls exhibited a reduced SPN. After delivery, male adolescents exhibited higher fP3 amplitudes to monetary compared with social incentives, whereas fP3 amplitudes in girls were comparable across incentive types. Moreover, whereas in boys fP3 responses were higher in rewards than in punishment trials, no such difference was evident in girls. The results indicate that adolescent boys show a reduced neural responsivity in the prospect of social punishment. Moreover, the findings imply that, once the incentive is obtained, adolescent boys attribute a relatively enhanced motivational significance to monetary incentives and show a relative hyposensitivity to punishment. The findings might contribute to our understanding of sex-specific vulnerabilities to problem behaviors related to incentive processing during adolescence.

Keywords Sex · Event-related potentials · Adolescence · Monetary · Social · Reward · Punishment · Incentive

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Electronic supplementary material The online version of this article (<https://doi.org/10.3758/s13415-018-0570-z>) contains supplementary material, which is available to authorized users.

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Introduction

Adequate processing of reward and punishment is crucial for learning and adaptive behavior. In everyday life, rewards and punishments are often of a monetary (e.g., monetary bonus or fine) or social character (e.g., social praise or rejection). In the past years, there has been a growing interest in studying the neurobiological bases of both social and monetary incentive processing in healthy adolescents and adults (Foulkes & Blakemore, 2016; Sescousse, Caldú, Segura, & Dreher, 2013; van Duijvenvoorde, Peters, Braams, & Crone, 2016), thereby applying different methodological approaches, such as functional magnetic resonance imaging (fMRI), event-related potentials (ERPs), and positron emission tomography (PET). More recently, researchers have begun to investigate dysfunctions in the neural mechanisms underlying the processing of these types of incentives in youth and adults suffering from psychiatric disorders that affect the brain's reward system, such as social anxiety disorder, autism, or attention-

deficit/hyperactivity disorder (Kohls et al., 2013, 2014; Richey et al., 2014).

Why is it important to study sex differences in incentive processing during adolescence?

Despite the increased interest in the neural substrates of incentive processing, very little research has been devoted to the basic question of whether there are sex differences in the brain's responsiveness to social or monetary incentives in healthy individuals. Of note, studies focusing on healthy adolescents in this field of research are particularly scarce. However, research on the neural underpinnings of sex differences in social and monetary incentive processing during adolescence is important for the following reason: The brain's reward system undergoes major changes in the transitional phase between childhood and adulthood with adolescents showing an increased reactivity to social and nonsocial incentives (Foulkes & Blakemore, 2016; van Duijvenvoorde et al., 2016). Adolescence has been described as a developmental period where social signals (such as social approval) and interactions become increasingly important and motivationally relevant. There is accumulating evidence that adolescence is not only characterized by a neural hyperresponsivity to rewarding social stimuli such as happy faces but also by a heightened reactivity to social punishment signals (Bolling et al., 2011; for a review, see Foulkes & Blakemore, 2016). Of note, data suggests that girls particularly show an increased sensitivity to negative social cues during adolescence (Silk, Davis, McMakin, Dahl, & Forbes, 2012).

At the same time that substantial neural changes in the brain's responsivity to incentives occur, adolescence is a critical period for the onset of many psychiatric disorders that are characterized by disturbances in incentive processing. Many of these disorders go along with sex differences in prevalence (e.g., adolescent depression or substance use disorder Costello, Mustillo, Erkanli, Keeler, & Angold, 2003). Elucidating the neural substrates of social and monetary incentive processing during this age period in healthy individuals might help us to better understand why adolescents of one sex or the other are more vulnerable for developing certain forms of problem behaviors related to processing various kinds of incentives (such as risk-taking behavior) or - in the extreme case - psychiatric disorders (Giedd, 2008).

The monetary and social incentive delay task

Research suggests that the processing of both reward and punishment can be subdivided into an anticipatory and a consummatory phase (Knutson, Bhanji, Cooney, Atlas, & Gotlib, 2008). Both stages reflect a different psychological state and separately shape human behavior. The well-established monetary incentive delay task (MIDT; Knutson, Westdorp, Kaiser,

& Hommer, 2000) has been developed to investigate anticipation and consumption of monetary incentives within one experimental paradigm. In this simple button-press task, monetary incentives (e.g., monetary gains or losses) are announced by a condition-specific cue, and the respective incentive is delivered depending on the participants' ability to respond to a target in time. This task has also been applied to investigate social incentive processing (social incentive delay task, SIDT) (Kohls et al., 2013; Rademacher et al., 2010; Spreckelmeyer et al., 2009), with several previous studies using happy and angry facial displays as social reward and punishment stimuli, respectively (Cremers, Veer, Spinhoven, Rombouts, & Roelofs, 2014; Kohls, Peltzer, Herpertz-Dahlmann, & Konrad, 2009; Nawijn et al., 2017; Spreckelmeyer et al., 2009). Positive and negative facial expressions belong to the most relevant nonverbal signals in communication and are incentives that modulate the probability that a certain behavior will occur in the future (Blair, 2003). Happy facial expressions encourage approach behavior and are perceived as rewarding, while angry faces have been shown to induce threat and activate avoidance behavior (Jaensch et al., 2014; Mühlberger et al., 2011). Studies that applied the SIDT have demonstrated that performance-contingent presentation of happy and angry faces modulates task performance as reflected by shorter reaction times relative to neutral trials/faces (e.g., Cremers et al., 2014; Spreckelmeyer et al., 2009), thus confirming the motivational relevance of these social stimuli.

Event-related potential correlates of incentive processing

Due to its high temporal resolution, event-related potential (ERP) studies are particularly well suited to examine the neural underpinnings of anticipatory and consummatory stages of incentive processing using the MIDT or SIDT (Broyd et al., 2012; Flores, Munte, & Donamayor, 2015). A commonly examined ERP component to study anticipatory processes is the stimulus-preceding negativity (SPN). The SPN is a slow cortical potential, which can be measured as a growing negativity reaching its maximum prior to the onset of a relevant stimulus, including an informative feedback (Foti & Hajcak, 2012). Several studies found the strongest SPN manifestation over centrotemporal and centroparietal regions, with a right hemispheric preponderance when a motivationally relevant feedback is provided (Kotani et al., 2003; Stavropoulos & Carver, 2013, 2014a, 2014b). The SPN is interpreted as a physiological index of expectancy or the salience of a feedback (Bocker, Brunia, & van den Berg-Lenssen, 1994; Brunia, Hackley, van Boxtel, Kotani, & Ohgami, 2011; Kotani et al., 2015). Further theories suggest that it may reflect anticipatory attention (thalamic gating model; Brunia, 1999) or the anticipation of the affective valence of the feedback (Bocker, Baas, Kenemans, & Verbaten, 2001; Bocker et al., 1994).

During the consummatory phase, the feedback-related negativity (FRN) and the feedback P3 (fP3) have been frequently studied. The frontocentral FRN emerges approximately 250 ms to 300 ms after the delivery of an informative feedback (Miltner, Braun, & Coles, 1997). This negative deflection is greater for perceived unfavorable compared with favorable incentives and has been suggested to represent a neural measure of the reward prediction error.¹ It is insensitive to the absolute magnitude of gains or losses and reflects the evaluation of binary outcomes (Gehring & Willoughby, 2002; Holroyd, Hajcak, & Larsen, 2006). Although the FRN has been typically studied in response to nonsocial/monetary incentives, recent work suggests that it also encodes social incentives (Stavropoulos & Carver, 2014b; Sun & Yu, 2014).

The fP3 is measured approximately 300 ms to 600 ms after incentive delivery and shows its maximum over the parietal region. It is associated with the motivational significance of the incentive. Moreover, it has been suggested that the fP3 reflects the amount of captured attentional resources (Nieuwenhuis, Aston-Jones, & Cohen, 2005). It is sensitive to both the magnitude (Yeung & Sanfey, 2004) and the valence of the incentive, although the latter finding is still controversially discussed (for a review, see San Martin, 2012).

Sex differences in the neural bases of social and monetary incentive processing

Despite their temporal strengths, ERP studies on sex differences in the neural underpinnings of social and monetary incentive processing based on the MIDT and the SIDT have been conducted neither in adolescents nor adults. However, two fMRI studies have combined the SIDT and MIDT in adults to study sex differences in anticipation (Spreckelmeyer et al., 2009) and consumption of monetary and social reward (Rademacher et al., 2010). The first study by Spreckelmeyer et al. (2009) found that men have a heightened reward circuit response to monetary rewards compared with females, and the opposite sex-related pattern was found for social rewards. This finding implies that men attribute a higher motivational value to prospective monetary incentives, while women perceive prospective social incentives as more significant. Interestingly, Rademacher et al. (2010) did not find sex differences in neural activation during the consumption phase. To date, it remains unclear as to what extent these findings can be generalized to adolescents.

¹ Research on the FRN difference wave scores this ERP as loss minus gain difference, resulting in a frontocentral negativity (e.g., Novak, Novak, Lynam, & Foti, 2016). Recently, it has been proposed to take the win minus loss difference instead (resulting in a frontocentral positivity, labeled “RewP”), following the emphasis current literature puts on the link between this component and reward sensitivity (Proudfit, 2015). The magnitude of the valence effect (win vs. loss) is the same in each case.

Insight from ERP studies on sex differences in social versus monetary incentive processing remains fragmentary as past research in adolescents or adults is restricted to studies using monetary incentives. Moreover, previous ERP studies (all applying gambling tasks) have exclusively focused on the consummatory phase, thereby reporting results on the FRN and the fP3. In regard of the FRN, some studies found larger amplitudes to monetary incentives in adolescent and adult males compared with females (Crowley et al., 2013; Yi et al., 2012), while other studies did not find sex differences or even enhanced FRN amplitudes in females when monetary incentives were delivered (Kamarajan et al., 2009; Santesso, Dzyundzyak, & Segalowitz, 2011). To our knowledge, only one study systematically investigated sex differences in healthy individuals in the fP3 (Grose-Fifer, Migliaccio, & Zottoli, 2014). This study found that adolescent boys compared with girls show a larger fP3 to monetary gains and losses during a gambling task, indicating that boys attribute a greater motivational significance to monetary incentives. Interestingly, the same study did not find fP3 amplitude differences between adult men and women, highlighting the difficulty in transferring findings from adult to adolescent populations.

The present study

Because insight into sex differences in the neurophysiology of social and monetary incentive processing among adolescents is particularly scarce, the aim of the present ERP study was to compare adolescent boys' and girls' ERP responses to social versus monetary incentive anticipation and consumption. Previous research suggests that adolescence is characterized by a heightened neural reactivity to rewards and to certain types of (social) punishment (Bolling et al., 2011; Foulkes & Blakemore, 2016; van Duijvenvoorde et al., 2016). However, it is largely unexplored as to whether sex differentially impacts on the neural processes underlying reward versus punishment processing in adolescence. Thus, another aim of this study was to examine this research question using ERPs. Insight into this field of research might improve our understanding of sex-specific susceptibilities to developmental risks related to incentive processing during adolescence (Giedd, 2008).

For this study, we combined the MIDT and the SIDT and examined the SPN during incentive anticipation, as well as the fP3 along with the FRN during incentive consumption. Based on previous findings (Spreckelmeyer et al., 2009), we hypothesized that girls compared with boys show a heightened neural sensitivity (i.e., a larger SPN) in the prospect of social rewards, while the reverse pattern was expected for monetary rewards. Moreover, we expected a reduced SPN in boys as opposed to girls in the prospect of punishment and, in particular, in the prospect of social punishment. This hypothesis was

based on related research showing that boys, compared with girls, show less punishment sensitivity (Pagliaccio et al., 2016) and less neural responsivity to negative social cues (Silk et al., 2012). Because of the scarce and inconsistent findings for the consummatory phase, no directed hypotheses were made for the FRN and fp3.

Method

Participants

Seventeen male and 21 female typically developing adolescents between 13 and 18 years of age were included in the study. Only participants with an IQ > 80 (based on the CFT-20-R; Weiß, 2006) were included. The two groups were comparable with regard to IQ, age, and handedness (see Table 1).

Participants were recruited via flyers and from a contact list containing names of families that had expressed interest in participating in studies within the department. In return for their participation, participants received vouchers. All participants were screened by experienced clinical psychologists to exclude psychiatric disorders using the Kinder-DIPS (Schneider, Unnewehr, & Margraf, 2009), which is a standardized semistructured interview for psychiatric disorders in children and adolescents. The Kinder-DIPS is a well-established German instrument with high retest reliabilities (Cohen's kappa = .85–.94) for all DSM-IV diagnoses. In addition, participants were screened for depressive symptoms using the *Beck Depression Inventory-II* (BDI-II; Beck, Steer, & Brown, 2006) and for psychopathological symptoms using the German version of the *Child Behavior Checklist* (CBCL/4-18) (Achenbach, 1993). Participants were only included in the study if they scored below the clinically relevant cutoff scores in the BDI-II and the CBCL. There were no significant differences between the groups in the BDI-II or the CBCL scores (all $ps > .05$; see Table 1).

Thirteen additional participants (four boys, nine girls) were initially assessed for eligibility but were not included in the present study as they fulfilled criteria for at least one psychiatric disorder based on the Kinder-DIPS and/or scored above the clinically relevant cutoff scores in the CBCL.

We applied the Behavior Inhibition System/Behavior Approach System scales (BIS/BAS scales; Carver & White, 1994; German version by Strobel, Beauducel, Debener, & Brocke, 2001) that were modified as a parental report (Blair, Peters, & Granger, 2004) to assess individual differences in personality dimensions that reflect the sensitivity of two self-regulatory systems: The BAS supporting approach motivation (Carver & White, 1994) and the BIS supporting the identification of goal conflict and serving to inhibit ongoing behavior. While the groups did not differ in BAS scores, girls showed

marginally higher BIS scores (see Table 1), which is in line with the literature (Pagliaccio et al., 2016).

None of the participants received any psychotropic medication or suffered from any relevant neurological or somatic disorders. The study was approved by the institutional review board of the Medical Faculty of the University Hospital Munich and was performed in accordance with the latest version of the Declaration of Helsinki and in compliance with national legislation. All participants were informed in detail about the experimental procedures and the aims of the study, and they provided written informed assent. Written informed consent was obtained by at least one parent/legal custodian, after the parent(s)/legal custodian(s) had been informed about all aspects of the study.

Experimental setup and procedure

In this study, we applied the MIDT and the SIDT (modified from Spreckelmeyer et al., 2009). The experiment comprised the following four conditions, which were presented blockwise: “monetary reward” (MR), “monetary punishment” (MP), “social reward” (SR) and “social punishment” (SP). Presentation order of the conditions was counterbalanced across participants. The two monetary and the two social conditions were always grouped together, resulting in eight possible presentation orders.

Each condition block (i.e., MR, MP, SR, and SP) consisted of 80 experimental trials, as well as 40 control trials serving as a baseline condition. Each of the 80 experimental trials per condition offered two possible outcomes (MR and SR conditions: “reward” vs. “no reward”; MP and SP conditions: “punishment” vs. “no punishment”), dependent on whether the participant managed to hit a target symbol in time, which was preceded by a condition-specific cue stimulus.

Each trial started with the presentation of a cue (see Fig. 1). The cue was presented for 500 ms and signaled to the participants whether the upcoming trial was an experimental or a control trial. The interstimulus interval (ISI) between the cue offset and the target was jittered between 1750 ms and 2250 ms (mean = 2,000 ms). The jittered ISI was intended to prevent an automated response and to ensure that the participants' attention was focused on the upcoming target. The task of the participants was to respond to the target by pressing a button with the dominant hand as fast as possible. Button presses during target presentation were counted as hits and resulted in a positive outcome during experimental trials (i.e., “reward” MR/SR conditions and “no punishment” in MP/SP conditions). Late button presses after the target had disappeared led to a negative outcome in experimental trials (i.e., “no reward” in MR/SR conditions and “punishment” in MP/SP conditions). Similarly, anticipatory reactions (i.e., reactions before target appearance) and omissions were followed by a negative outcome in experimental trials. Target

Table 1 Demographic and behavioral characteristics of the groups

	Females ($n = 21$)	Males ($n = 17$)	p
Age (M, SD)	16.06 (1.43)	15.58 (1.36)	.30
Age range (min–max)	13.20–18.70	13.10–17.22	
IQ (M, SD)	107.95 (8.67)	103.71 (11.91)	.21
IQ range (min–max)	95–125	85–125	
Handedness (right/left)	20/1	17/0	.37
BDI-II (M, SD)	3.67 (3.92)	2.06 (2.93)	.17
CBCL total T score (M, SD)	47.32 (7.17)	47.07 (8.93)	.99
BAS Drive score	11.37 (1.64)	11.33 (1.88)	.95
BAS Fun score	10.26 (1.76)	10.80 (2.08)	.42
BAS Reward score	15.16 (1.80)	14.67 (1.29)	.38
BIS score	18.47 (1.61)	17.27 (2.40)	.09

BDI-II = *Beck Depression Inventory–II*; CBCL = *Child Behavior Checklist*; BAS = Behavioral Approach System; BIS = Behavioral Inhibition System. Higher values in the BDI-II, the CBCL and the BIS/BAS scales represent a higher manifestation of the symptoms/behavioral tendencies measured

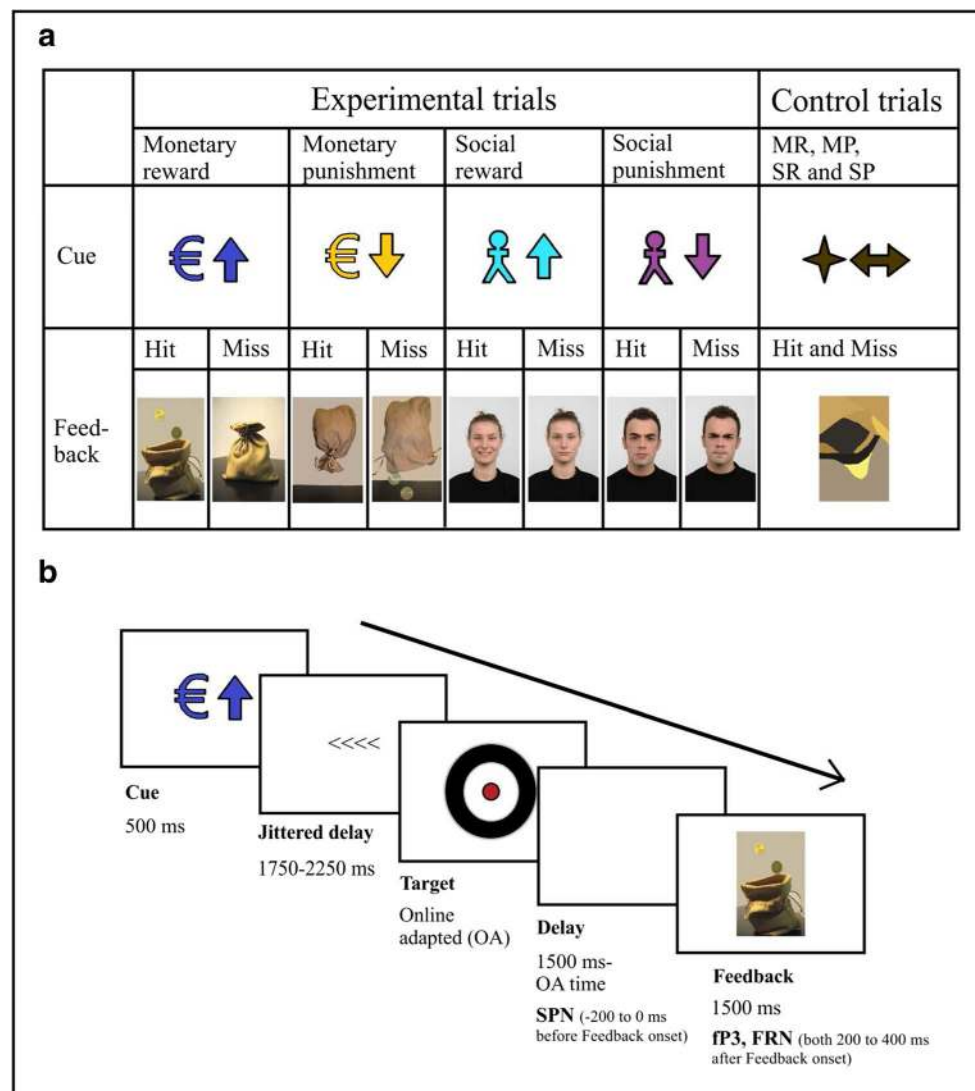


Fig. 1 **a** Design and stimuli (cue/feedback) of the experimental paradigm. **b** Trial structure (e.g., monetary reward condition, positive outcome) and time windows for the event-related potentials

duration was set individually based on an online algorithm (see next paragraph). In control trials, participants always received an uninformative outcome (i.e., scrambled picture) regardless of their performance. The outcome was presented 1,500 ms after target onset and remained on the screen for 1,500 ms. Given that the outcome onset was independent of the individual reaction times (RTs), trial duration was kept constant. The intertrial interval was set at 500 ms.

The individual response window (i.e., the period of time while the target remained onscreen) was defined through an online response algorithm (for a similar approach, see, e.g., Kohls, Perino, et al., 2013). The initial target durations for each condition were based on the individual mean RTs in a practice block, which preceded the experimental block and helped to familiarize the participant with the task. During the experiment, the target duration was adjusted online based on the RTs of the two previous experimental trials to achieve an accuracy rate of ~50% (see Foti & Hajcak, 2009; Santesso et al., 2011). In more detail, the response window/target duration equaled the mean RT of the two previous experimental trials. In case one of the two previous experimental trials was invalid due to an anticipatory reaction or an omission, the new target duration equaled the remaining response. If both previous responses were invalid, the target duration remained unchanged. Note that this online algorithm also defined the target duration for the respective control trials in each block, although the calculation of the target duration was exclusively based on the two previous experimental trials.

Aligning all subjects to an accuracy rate - and thus positive outcome rate - of approximately 50% (i.e., ~50% win-loss ratio) has been shown to be optimal with regard to the motivational value (Williams, Whiten, Suddendorf, & Perrett, 2001) as it guarantees that positive and negative outcomes are presented in the same frequency. The online algorithm furthermore promoted task believability, as actual outcomes are clearly linked to the specific reaction within each trial. Importantly, a manipulation check at the end of the experiment confirmed that all participants perceived the received outcome within each trial as performance contingent. The hit rate of the participants across groups in experimental trials was on average $46.2\% \pm 3.5\%$ (approximating the targeted 50%). Notably, groups did not differ in hit rates in any of the experimental conditions (all $ps \geq .09$).

Before the start of each block, extensive oral and visually animated task instructions were given, and participants were informed about the nature of the incentives in the forthcoming block (i.e., whether a MR, MP, SR, or SP block followed). The participants were also informed that the four possible outcomes (“reward” “no reward,” “punishment,” “no punishment”) within the monetary conditions were not only represented by diverse, particular outcome stimuli but also by gain, no gain, loss, or no loss of real money. In the MR block, participants were informed that each positive outcome would

result in monetary gain (+0.20€), whereas each negative outcome meant a missed opportunity to gain 0.20€. Likewise, in the MP block, participants were told that each negative outcome would result in the loss of 0.20€ (from a starting value of 8€), whereas each positive outcome picture meant avoiding a loss of 0.20€. Thus, based on the win-loss ratio of approximately 50%, participants could earn a bonus of approximately 8€ in total (~8€ win in the monetary reward block; 8€ starting value in the monetary punishment block; ~8€ loss in the monetary punishment block). For reasons of comparability, participants’ bonus was rounded up to 10€ at the end of the testing (for a similar approach, see Broyd et al., 2012; Kohls et al., 2011).

Response collection and stimulus presentation was controlled by the software E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). All stimuli were presented on a 17-inch Dell monitor, placed 70 cm in front of the subjects.

Experimental stimuli

The outcome stimuli (see Fig. 1) of the MR and MP conditions were designed to suit the themes of monetary reward (“reward” vs. “no reward”) and punishment (“punishment” vs. “no punishment”). Altogether, 40 slightly varying photographs of money bags were presented (10 for each outcome type: reward/no reward; punishment/no punishment). The variation in the photographs included slight differences in the form and posture of the money bags and were intended to mirror variations between the individual facial stimuli of the social conditions as described below.

The outcome stimuli for the SR and SP conditions were chosen to suit the themes of social reward/no reward (happy vs. neutral faces) and social punishment/no punishment (angry vs. neutral faces) (see Fig. 1). The pictures of the faces were derived from the Radbound database (Langner et al., 2010) and comprised 40 different stimuli (10 for each outcome type: reward/no reward; punishment/no punishment). More precisely, the stimuli consisted of photographs of 10 Caucasian models showing happy (reward) versus neutral faces (no reward) and 10 Caucasian models demonstrating angry (punishment) versus neutral faces (no punishment).

The 40 control trials within each block consisted of 10 slightly varying scrambled patterns (designed with Adobe Photoshop 7.0). The stimuli in the social and monetary conditions and the control stimuli were comparable with regard to luminance. Both the two condition-specific cue stimuli (designed with Adobe Photoshop 7.0) as well as the control cue stimulus consisted of an array of a symbol and an arrow.

EEG recordings and data processing

During the experiment, EEG was recorded using an Electrical Geodesic Inc. 128-channel system, with a sampling rate of

500 Hz and Cz as the reference electrode (see Fig. 2). The impedance was kept below 50 k Ω during recording.

Further processing steps were performed with Brainvision Analyzer 2.0 (Brain Products GmbH, Gilching, Germany). After visual inspection of the data and off-line filtering with a 0.53 (time constant 0.3) to 30 Hz band pass (Butterworth zero phase, 12 dB/Oct) and 50 Hz notch filter, independent component analysis (ICA) was run to remove electrooculogram (EOG) artifacts. Subsequently, all electrodes were referenced to the averaged mastoids (Electrode 57 and 100 in Fig. 2). Artifacts apart from EOG artifacts were defined as amplitudes exceeding +100 μ V, bursts of electromyographic activity (maximal allowed voltage step: 50 μ V/ms), and any activity lower than 0.5 μ V in intervals of 100 ms. These artifacts were also excluded from further processing (individual channel mode).

Data analysis

Behavioral data

RTs of the experimental trials were entered into a 2 (sex) \times 2 (task modality) \times 2 (outcome modality) mixed-model ANOVA, with sex as a between-subjects factor and task modality and outcome modality as within-subjects factors. RTs of the control trials were compared between the sex groups separately for each condition using independent-samples *t* tests. To mirror the analysis approach of the ERP data analysis described below, invalid responses (anticipatory reactions,

responses faster than 100 ms or slower than 700 ms) were not included in the analysis of RTs for experimental and control trials. Furthermore, in order to validate the motivational value of the experimental outcomes, RTs in control trials were compared with the RTs in the experimental trials separately for each condition (MR, MP, SR, and SP) and group using paired-samples *t* tests.

ERP data

Positive outcome trials were defined as trials with button presses within the presentation duration of the target (positive outcome valence). Negative outcome trials were defined as trials with responses after the target had disappeared from the screen (negative outcome valence). Anticipatory reactions (before the target was onscreen) and trials with missed button presses were not included in further analyses, although these responses were followed by a negative outcome in experimental trials. Additionally, trials with responses faster than 100 ms or slower than 700 ms were not included. The rationale for this approach was that the neural mechanisms underlying these invalid responses might not be linked to incentive processing per se but might have been caused by distraction, thus differing from the mechanism underlying valid responses.

The continuous EEG was segmented into epochs (stimulus-locked ERPs). Segments for the SPN were defined from –600 ms to 100 ms before the outcome onset, with the signal between –600 ms and –400 ms serving as baseline. For the analysis of the SPN, ERPs were averaged separately for the four experimental conditions (MR, MP, SR, SP). Control trials were not included in the SPN analysis, as this component is only elicited in the prospect of informative feedback stimuli (Böcker, Brunia, & van den Berg-Lenssen, 1994; Foti & Hajcak, 2012). Based on visual inspection of the data and on previous reports demonstrating that the SPN is strongest over right lateralized central regions (Masaki, Takeuchi, Gehring, Takasawa, & Yamazaki, 2006; Stavropoulos & Carver, 2014a), two lateralized central ROIs were defined approximating the locations of C3 and C4 (see Fig. 2). The left central ROI included the electrodes 30, 36, 37, 41, 42, and 47; the right central ROI included the electrodes 87, 93, 98, 103, 104, and 105.

Segments for the fP3 and the FRN were defined from –200 ms to 1,000 ms related to the outcome onset, with the 200 ms prestimulus interval used for baseline correction. For the fP3 analysis, ERPs were averaged separately for negative and positive outcome trials in the four conditions. Control trials were not included in the final ERP analyses (see Santesso et al., 2011), as the fP3 components for the control trials were characteristically different from informative outcome trials, with peaks emerging much earlier than during the typical fP3 window (see Supporting Material 1 for a descriptive illustration). The FRN was reliably elicited in the

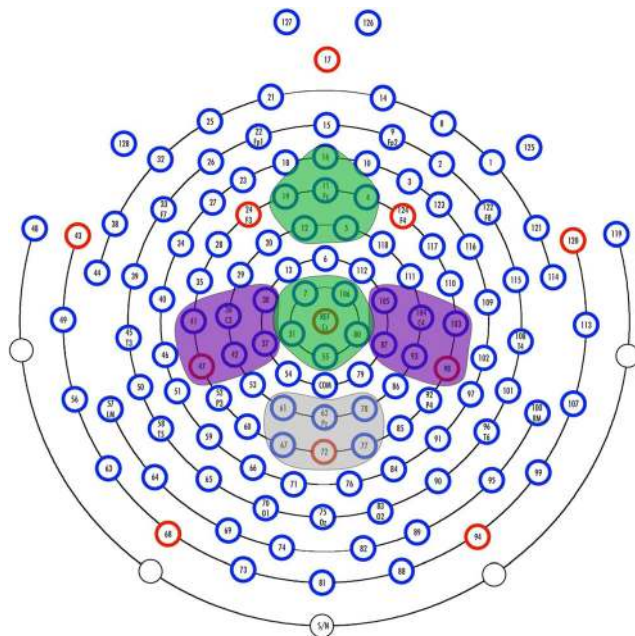


Fig. 2 Electrical Geodesic Inc., 128-channel system: Regions of interest (ROI) were defined (1) for the SPN over two lateralized central regions (purple), (2) for the fP3 over a parietal region (gray), and (3) for the FRN over a frontal and a central region (green). (Color figure online)

monetary conditions but could not be reliably detected in the social conditions (see Sun & Yu, 2014). Therefore, analysis for this component was restricted to the monetary conditions, and ERPs were averaged separately for negative and positive outcome trials in the two monetary conditions MR and MP.

Based on visual data inspection and previous reports (Cox et al., 2015, Novak & Foti, 2015), the ROI for the fP3 included the parietal electrodes 61, 62, 67, 72, 77, and 78 (see Fig. 2). To allow for comparisons with previous studies on sex-related differences in the FRN (Grose-Fifer et al., 2014; Santesso et al., 2011; Yi et al., 2012), analyses were run with absolute FRN values instead of difference wave scores. For the FRN, we defined a frontal and a central ROI based on data inspection and previous literature (Novak, Novak, Lynam, & Foti, 2016). The frontal ROI was defined around Fz and the central ROI around Cz, spanning the electrodes 4, 5, 11 [Fz], 12, 16, 19 and 7, 31, 55, 80, 106, 129 [Cz], respectively (see Fig. 2).

With regard to all components, a minimum of ≥ 20 artifact-free trials per condition/outcome for each of the electrodes included in the ROI was necessary. All participants included in the final sample (see [Participants](#) section) met this criterion. Five additional participants (two boys, three girls) were initially tested but not included in the final sample (see [Participants](#) section), as they did not fulfill this criterion. Group means for the number of trials included in the SPN analyses were >32 trials for all experimental conditions. With regard to the fP3 and FRN, group means were >30 trials (fP3) and >30 trials (FRN) for all positive and for all negative outcome trials within each of the experimental conditions.

Within the particular ROI, ERPs were averaged across the respective electrodes for statistical analysis. Grand averages were computed separately for the male and female groups. Based on the literature and visual data inspection, for the SPN, mean activity values during the last 200 ms before outcome onset were exported for statistical analysis (Poli, Sarlo, Bortoletto, Buodo, & Palomba, 2007; Stavropoulos & Carver, 2014a). The time window used to determine individual peak amplitudes and latencies of the fP3 was set between 200 ms and 400 ms after outcome onset (based on visual inspection of the grand averages and on previous reports; Kamarajan et al., 2009; Santesso et al., 2011). To determine individual mean amplitudes of the FRN, the time window was set between 200 ms and 400 ms after outcome onset (see Santesso et al., 2011).

SPN mean values were analyzed based on a 2 (sex) \times 2 (laterality) \times 2 (task modality; i.e., monetary/social) \times 2 (outcome modality; i.e., reward/punishment) mixed-model ANOVA. FP3 peak amplitudes and latencies were analyzed based on a 2 (sex) \times 2 (task modality) \times 2 (outcome modality) \times 2 (outcome valence; i.e., positive/negative outcome) mixed-

model ANOVA. Finally, FRN mean difference amplitudes were analyzed using a 2 (sex) \times 2 (outcome modality) \times 2 (outcome valence) \times 2 (ROI) mixed-model ANOVA.

In case of significant group differences in ERP parameters, we further investigated brain-behavior relationships by examining correlations with behavioral inhibition (BIS scale) and behavioral approach (BAS reward scale) tendencies related to punishment and reward sensitivity, respectively. In addition, correlations between these ERP parameters and the CBCL total T score were computed. Correlations were calculated separately for both groups. To correct for multiple testing, the significance level was adjusted by applying the Bonferroni–Holm procedure.

Statistical analyses of both the ERP and behavioral data were conducted with IBM SPSS Statistics 23. For all analyses, the significance level was set to $p = .05$ (two-tailed). Values exceeding the mean of each group by more than 3 standard deviations were excluded from the analysis (less than 5% of the data was removed based on this procedure).

Because of the focus of the present study, significant interactions are reported only if they involve the factor sex. Significant interactions involving the factor sex were further investigated using post hoc t tests. When sphericity was violated in an ANOVA, the degrees of freedom were corrected using Greenhouse–Geisser’s procedure.

Results

Behavioral data

The behavioral data are summarized in Table 2. We found no significant main effect of sex, $F(1, 34) = 0.49$, $p = .49$; $\eta_p^2 = .02$, or outcome modality (reward or punishment), $F(1, 34) = 1.65$, $p = .21$, $\eta_p^2 = .04$, on RTs. Task modality (social or monetary) significantly influenced RTs, $F(1, 34) = 12.85$, $p < .01$, $\eta_p^2 = .21$, such that across both groups RTs were faster in monetary trials (233.13 ± 23.68 ms) than in social trials (243.04 ± 27.99 ms).

In all four blocks, RTs of control trials were comparable between male and female participants (all $ps \geq .25$; see Table 2). RTs between experimental and control trials differed significantly within all four blocks for both groups (all $ps < .001$): RTs for experimental trials were significantly shorter than for control trials, thus confirming the motivational value of the informative outcome in experimental trials.

Electrophysiological data

Group means of ERP parameters are reported in Table 3.

Table 2 Reaction times in ms (mean, *SD*) in experimental and control trials listed separately for each block and each gender group

Trial type	Block type	Females (<i>n</i> = 21)	Males (<i>n</i> = 17)	<i>p</i>
Experimental trials	Monetary reward	229.84 (19.49)	234.74 (28.08)	.54
	Monetary punishment	231.86 (17.66)	243.26 (42.18)	.31
	Social reward	240.43 (22.71)	253.61 (44.12)	.24
	Social punishment	246.14 (29.27)	253.90 (46.80)	.54
Control trials	Monetary reward	256.47 (38.20)	263.63 (47.57)	.61
	Monetary punishment	260.56 (41.47)	260.98 (42.79)	.98
	Social reward	251.53 (17.32)	267.41 (53.41)	.25
	Social punishment	256.78 (27.01)	269.29 (40.31)	.26

Table 3 Group means of event-related potentials: **a** stimulus preceding negativity (SPN), **b** feedback P3 (fP3) and **c** feedback-related negativity (FRN)

a	Females (<i>n</i> = 21)	Males (<i>n</i> = 17)	Females (<i>n</i> = 21)	Males (<i>n</i> = 17)
SPN			SPN	
<i>Amplitude (μV)</i>			<i>Amplitude (μV)</i>	
<i>left hemisphere</i>			<i>right hemisphere</i>	
Mon. reward	−0.74 (0.71)	−0.75 (1.54)	Mon. reward	−1.44 (1.45)
Mon. punishment	−0.28 (1.36)	−0.29 (1.88)	Mon. punishment	−1.18 (0.93)
Soc. reward	−0.53 (0.99)	−0.89 (2.53)	Soc. reward	−1.43 (0.89)
Soc. punishment	−0.92 (1.05)	0.16 (2.06)	Soc. punishment	−1.62 (1.39)
b	Females (<i>n</i> = 21)	Males (<i>n</i> = 17)	Females (<i>n</i> = 21)	Males (<i>n</i> = 17)
fP3			fP3	
<i>Amplitude (μV)</i>			<i>Latency (ms)</i>	
<i>positive outcome</i>			<i>positive outcome</i>	
Mon. reward	11.73 (4.17)	18.95 (8.41)	Mon. reward	294.75 (33.82)
Mon. punishment	8.75 (4.54)	15.40 (8.80)	Mon. punishment	302.51 (35.74)
Soc. reward	8.03 (4.06)	12.79 (7.61)	Soc. reward	282.98 (34.50)
Soc. punishment	8.66 (4.86)	11.29 (6.35)	Soc. punishment	278.02 (33.05)
fP3			fP3	
<i>Amplitude (μV)</i>			<i>Latency (ms)</i>	
<i>negative outcome</i>			<i>negative outcome</i>	
Mon. Reward	8.47 (3.18)	15.32 (7.49)	Mon. Reward	288.10 (42.29)
Mon. Punishment	9.31 (4.12)	13.64 (8.23)	Mon. Punishment	294.46 (36.16)
Soc. Reward	7.78 (3.58)	10.97 (5.34)	Soc. Reward	301.08 (50.40)
Soc. Punishment	9.02 (5.85)	11.38 (5.60)	Soc. Punishment	277.03 (44.71)
c	Females (<i>n</i> = 21)	Males (<i>n</i> = 17)	Females (<i>n</i> = 21)	Males (<i>n</i> = 17)
FRN			FRN	
<i>Amplitude (μV)</i>			<i>Amplitude (μV)</i>	
<i>frontal ROI</i>			<i>central ROI</i>	
<i>positive outcome</i>			<i>positive outcome</i>	
Mon. reward	−3.09 (4.37)	−4.08 (5.85)	Mon. reward	5.35 (4.25)
Mon. punishment	−2.53 (4.24)	−3.62 (5.22)	Mon. punishment	4.61 (4.42)
FRN			FRN	
<i>Amplitude (μV)</i>			<i>Amplitude (μV)</i>	
<i>frontal ROI</i>			<i>central ROI</i>	
<i>negative outcome</i>			<i>negative outcome</i>	
Mon. reward	−3.90 (4.36)	−6.57 (3.90)	Mon. reward	3.03 (4.51)
Mon. punishment	−3.98 (3.48)	−5.12 (4.85)	Mon. punishment	3.72 (4.30)

Stimulus-preceding negativity (SPN)

We found no significant effect of sex, $F(1, 34) = 0.44$, $p = .51$, $\eta_p^2 = .01$; task modality, $F(1, 34) = 0.00$, $p = .97$, $\eta_p^2 = .00$; or outcome modality, $F(1, 34) = 3.29$, $p = .08$, $\eta_p^2 = .09$, on the SPN amplitude. The main effect of laterality was significant, $F(1, 34) = 38.90$, $p < .001$, $\eta_p^2 = .53$. Mean SPN activity was more negative over the right hemisphere ($-1.32 \pm 1.29 \mu\text{V}$) than over the left hemisphere ($-0.54 \pm 1.03 \mu\text{V}$).

We found a significant Task Modality \times Outcome Modality \times Sex interaction, $F(1, 34) = 6.39$, $p < .05$, $\eta_p^2 = .16$. Post hoc comparisons of the two groups revealed a significant group difference in the SP (social punishment) condition, $t(35) = 2.11$, $p < .05$, but not in the other experimental conditions (all $ps > .05$). In the SP condition, girls ($-1.34 \pm 0.89 \mu\text{V}$) had significantly more negative SPN mean values than boys did ($-0.21 \pm 1.89 \mu\text{V}$). Inspection of Fig. 3 suggested that this difference between boys and girls predominantly arose from reduced SPN values in boys in the social punishment compared with the other conditions, whereas girls showed little modulation across conditions. Exploratory within-group comparisons to quantify this visual impression showed that boys exhibited a reduced SPN in the social punishment compared with the social reward condition ($p < .05$; all $ps \geq .16$ for the remaining comparisons). By contrast, in girls, SPN values in the social punishment condition did not significantly differ from the remaining conditions (all $ps \geq .068$). All remaining interactions involving the factor sex (including the four-way interaction) were nonsignificant (all $ps \geq .07$).

Feedback P3

Feedback P3 amplitude

There was a significant main effect of sex on fP3 amplitudes, $F(1, 36) = 8.41$, $p < .01$, $\eta_p^2 = .19$. Boys ($13.72 \pm 6.32 \mu\text{V}$) exhibited higher amplitudes than girls did ($8.97 \pm 3.66 \mu\text{V}$). Besides, significant main effects of outcome (positive, negative), $F(1, 36) = 10.63$, $p < .01$, $\eta_p^2 = .23$; task modality, $F(1, 36) = 17.46$, $p < .001$, $\eta_p^2 = .33$; and outcome modality, $F(1, 36) = 5.70$, $p < .05$, $\eta_p^2 = .14$, were revealed. Amplitudes were higher in response to a relatively positive ($11.67 \pm 5.92 \mu\text{V}$) compared with a relatively negative outcome ($10.52 \pm 5.30 \mu\text{V}$). Furthermore, larger fP3 amplitudes were revealed in monetary ($12.37 \pm 6.64 \mu\text{V}$) than in social blocks ($9.82 \pm 5.03 \mu\text{V}$). Finally, fP3 amplitudes were larger in reward conditions ($11.46 \pm 5.49 \mu\text{V}$) compared with punishment conditions ($10.72 \pm 5.73 \mu\text{V}$).

A significant interaction between task modality and sex was revealed, $F(1, 36) = 5.47$, $p < .05$, $\eta_p^2 = .13$. Post hoc within-group comparisons showed that monetary ($15.83 \pm 7.89 \mu\text{V}$) compared with social incentives ($11.61 \pm 5.40 \mu\text{V}$) elicited significantly larger fP3s in adolescent boys, $t(16) = 3.63$, $p < .01$ (see Fig. 4; for a more detailed illustration, see Supporting Material 2); by contrast, girls exhibited only a marginal significant difference in fP3 amplitudes between monetary ($9.56 \pm 3.65 \mu\text{V}$) and social incentives ($8.37 \pm 4.29 \mu\text{V}$), $t(20) = 1.73$, $p = .09$. Moreover, a significant interaction between sex and outcome modality was found, $F(1, 36) = 4.85$, $p < .05$, $\eta_p^2 = .12$. In boys, fP3 amplitudes were significantly higher in reward ($14.51 \pm 6.28 \mu\text{V}$) than in punishment conditions ($12.93 \pm 6.58 \mu\text{V}$), $t(16) = 2.70$, $p < .05$.

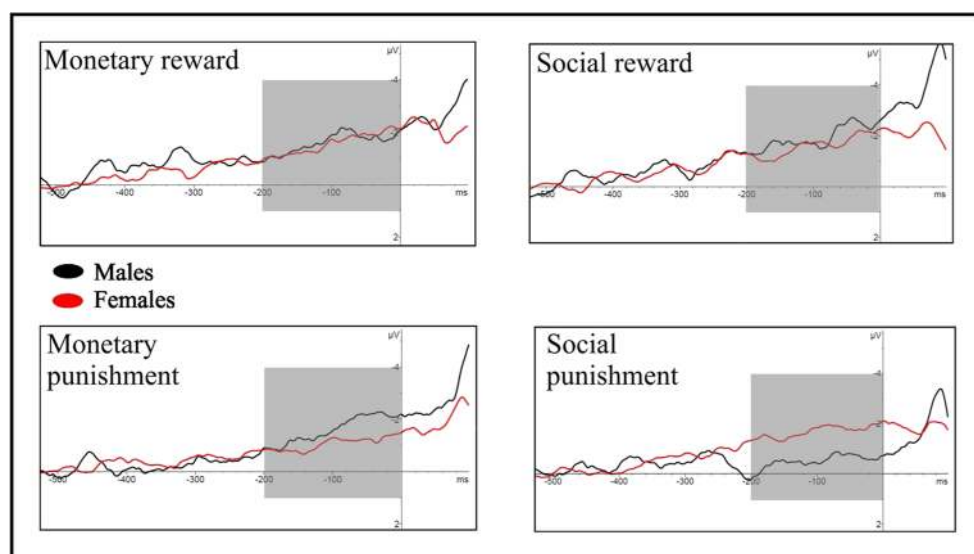


Fig. 3 Stimulus-locked event-related potential (stimulus-preceding negativity, SPN) preceding incentive delivery for males (black) and females (red). The gray windows depict the time window used to determine mean activity values of the SPN. (Color figure online)

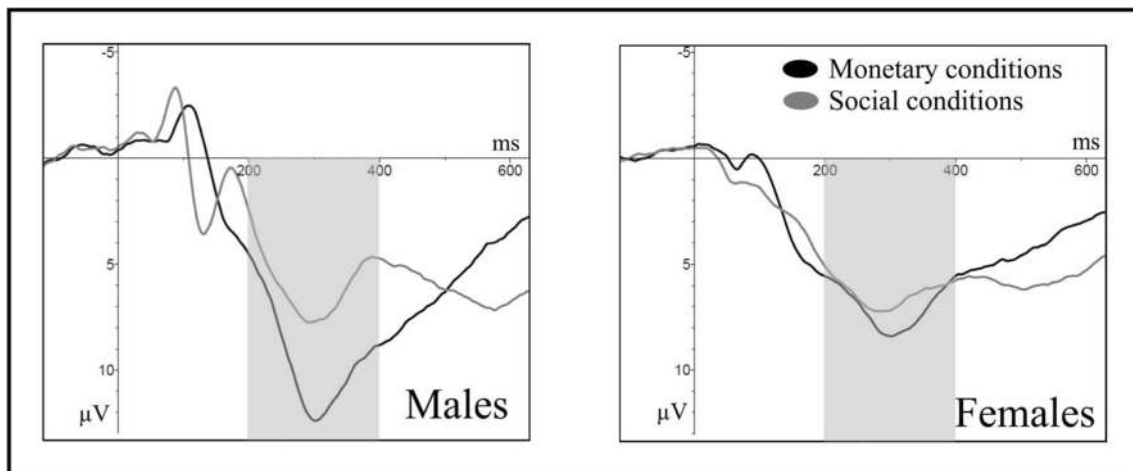


Fig. 4 Stimulus-locked event-related potential (feedback P3; fP3) following social (gray) and monetary incentive delivery (black) for males (left) and females (right), averaged across feedback modality

(reward, punishment) and outcome valence (positive vs. negative outcome). Gray windows depict the time window used to determine individual peak amplitudes and latencies of the fP3

(see Fig. 5; for a more detailed illustration, see Supporting Material 2). In girls, the difference in fP3 amplitudes between reward ($9.00 \pm 3.15 \mu\text{V}$) and punishment conditions ($8.94 \pm 4.31 \mu\text{V}$) was nonsignificant, $t(20) = 0.16$, $p = .87$. All other interactions involving the factor sex were nonsignificant (all $ps \geq .14$).

Feedback P3 latency

We found no significant main effects on fP3 latencies (all $ps \geq .10$). Moreover, all interactions involving the factor sex were not significant (all $ps \geq .10$).

Feedback-related negativity (FRN)

FRN amplitudes were comparable across groups, $F(1, 36) = 1.22$, $p = .27$, $\eta_p^2 < .03$, and outcome modality, $F(1, 36) = .72$, $p = .40$, $\eta_p^2 = .02$. The main effect of ROI was significant, $F(1, 36) = 214.96$, $p < .001$, $\eta_p^2 = .86$, with higher FRN amplitudes across the frontal ($-4.03 \pm 4.17 \mu\text{V}$) compared with the central site ($3.38 \pm 5.32 \mu\text{V}$). A significant main effect of outcome valence was revealed, $F(1, 36) = 26.93$, $p < .001$, $\eta_p^2 = .43$, with more negative amplitudes for negative ($-1.23 \pm 4.26 \mu\text{V}$) compared with positive outcomes ($0.58 \pm 5.03 \mu\text{V}$). None of the interactions involving the factor sex reached significance (all $ps \geq .13$).

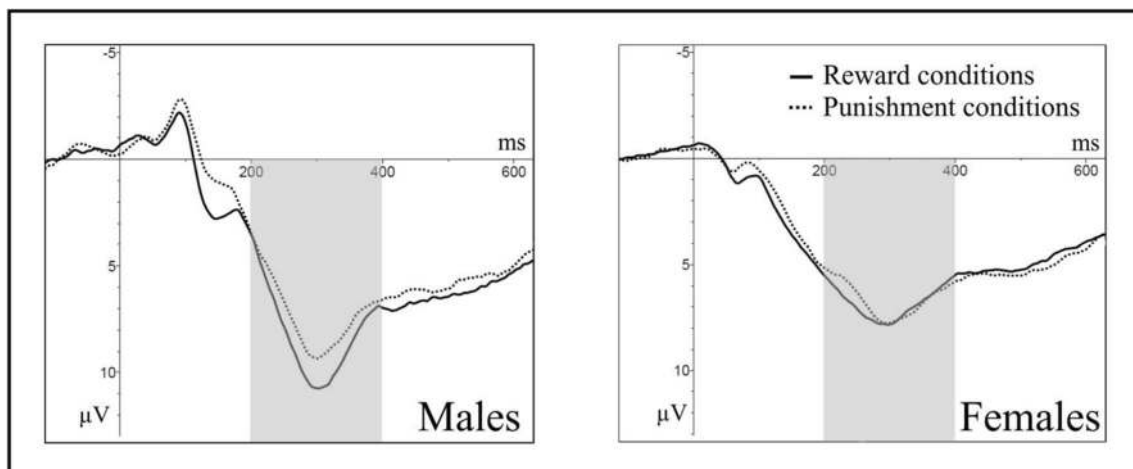


Fig. 5 Stimulus-locked event-related potential (feedback P3; fP3) following incentive delivery in the reward (solid line) and the punishment (dotted line) conditions for males (left) and females (right), averaged across task modality (social, monetary) and outcome valence

(positive vs. negative outcome). The gray windows depict the time window used to determine individual peak amplitudes and latencies of the fP3

Brain-behavior relationships

To examine brain-behavior relationships, SPN mean values, and the difference scores of fP3 amplitudes to (a) monetary versus social incentives and (b) rewards versus punishment were correlated with the CBCL total *T* score, the BIS and the BAS reward score, respectively (separately for both groups). Difference scores were computed regarding the fP3 amplitude for (a) and (b) as ERP analyses revealed within-group differences between the respective conditions. These correlational, Bonferroni–Holm corrected analyses revealed nonsignificant results (all $p_s \geq .13$).

Discussion

The aim of the present study was to examine sex differences in the neurophysiological correlates of monetary and social incentive processing in adolescence. Sex differences were revealed in both the anticipatory (SPN) and the consummatory (fP3) phase. We found that during anticipation of social punishment, adolescent boys, compared with girls, exhibited a reduced SPN. In regard of the consummatory phase, the results revealed that in male adolescents, monetary outcome resulted in larger fP3 amplitudes than social outcome did, while fP3 amplitudes in girls were comparable across both outcome types. Moreover, while in boys fP3 waves were higher in response to rewards than to punishment, no such effect was seen in girls.

Behavioral data

The MIDT and the SIDT are frequently used to study neural and behavioral mechanisms of incentive processing, as these tasks provide important insights into a person's motivation to gain reward or avoid punishment (Broyd et al., 2012). For both the monetary and the social conditions, the behavioral data showed clear motivational effects for both groups, as RTs were faster following cues signaling potential punishment or reward compared with the control condition. This is in line with the literature (Knutson et al., 2000; Spreckelmeyer et al., 2009) and indicates the engagement of effortful response processes to achieve a better performance and a relatively positive outcome (Broyd et al., 2012; Dillon & Pizzagalli, 2013).

Despite group differences on the neural level, male and female adolescents demonstrated comparable behavioral performance in the social and monetary conditions, which mirrors a previous study in adults (Barman et al., 2015). As neurobiological measures can be more sensitive than behavior (Wilkinson & Halligan, 2004), comparable behavioral performance is not contradictory to the observed group differences in the neurophysiological data.

ERP data

Anticipation of reward and punishment: Stimulus preceding negativity

To our knowledge, the present study is the first to examine sex differences in neural processes underlying anticipation of both social and nonsocial monetary reward and punishment in adolescence. We found a decreased SPN in boys compared with girls, and, interestingly, this differential brain response between the sexes was restricted to the social punishment condition. Of note, inspection of the neurophysiological result patterns suggested that this difference between the sexes mainly arose from a hyporesponsivity in boys to this kind of incentive rather than a hypersensitivity to social punishment in girls. The SPN is involved in salience processing (Kotani et al., 2015) and has been suggested to reflect anticipatory attention (Brunia, 1999). In line with these assumptions, the SPN is increased when individuals anticipate motivationally relevant outcomes, particularly if the outcome is performance contingent (Brunia et al., 2011), as it was the case in the present study. Accordingly, our finding of a reduced SPN in the social punishment condition in boys likely reflects that social punishment has a low salience for this group. The announcement of this type of outcome appears to be processed with little priority and captures decreased anticipatory attention in male compared with female adolescents.

Based on the SIDT applied in the present study, a social situation was created in which the own performance was evaluated. It is suggested that the prospect of angry faces in the social punishment condition induced interpersonal threat. This view is supported by research showing that angry faces are perceived as threatening (Mühlberger et al., 2011). Moreover, an angry face is an evolutionary fear-relevant stimulus that provokes a fear response (Öhman, 1986; Roelofs, Hagens, & Stins, 2010) and activates threat-related brain structures, including the insula (Mühlberger et al., 2011; for a review see Fusar-Poli et al., 2009). On a more global level, the reduced neural responsiveness of boys during the anticipation of (potential) social punishment can be linked to research showing that adolescent boys perceive less interpersonal threat and show a reduced sensitivity to (negative) evaluation compared with girls (Silk et al., 2012; Zubeidat, Salinas, & Sierra, 2008).

A decreased sensitivity to social punishment signals has previously been shown in male adolescents with early-onset conduct disorder (Fairchild, Van Goozen, Calder, Stollery, & Goodyer, 2009) and in men with antisocial personality disorder (Schönenberg, Louis, Mayer, & Jusyte, 2013). In future large-scaled studies including children, adolescents, and adults, it would be worthwhile to explore whether decreased neurophysiological sensitivity during the anticipation of social punishment might represent a potential vulnerability factor for

early-onset CD and antisocial personality disorder and whether sex differences in this domain might contribute to the male preponderance of these disorders (Eme, 2007).

In contrast to our expectations and the findings in adults (Spreckelmeyer et al., 2009), we found no sex differences regarding the neurophysiological processes during the anticipation of social or monetary rewards, suggesting that the prospect of these types of reward had a comparable motivational relevance for male and female adolescents in our sample. Besides the divergent methodological approach of the two studies, one reason for the discrepant findings might relate to differences in the age group investigated. This aspect is important as there is evidence suggesting substantial developmental changes in the neural substrates underlying incentive processing from adolescence to adulthood, which might result in differential findings regarding sex differences in adolescence versus adulthood (Grose-Fifer et al., 2014). Moreover, Spreckelmeyer et al. (2009) varied the reward magnitude of both the social and monetary incentives, which was not the case in the present study. This difference in the study design might be of particular importance with regard to the monetary reward condition, as it has been reported that males show an enhanced neural responsivity, particularly in the prospect of high monetary rewards (Grose-Fifer et al., 2014; Spreckelmeyer et al., 2009). In future studies, it would be important to study sex differences during the anticipation of various levels of monetary and social rewards in children, adolescents, and adults using the same methodological framework. Such an approach would help to disentangle to what extent sex differences in the neural processes underlying the anticipation of monetary incentives differ depending on the specific developmental period studied or the anticipated reward magnitude.

Consumption of reward and punishment: Feedback P3 and feedback-related negativity

In contrast to girls, boys exhibited larger fP3 amplitudes in response to monetary versus social incentives. It has been shown that the fP3 is predominantly influenced by stimulus salience (Novak & Foti, 2015), and prior reports suggest that this component reflects the allocation of attentional resources (Nieuwenhuis et al., 2005) and the motivational significance of an outcome (Yeung & Sanfey, 2004). Thus, the present data suggest that boys attach more relevance to monetary than to social incentives *once the incentive is obtained*. By contrast, girls seem to process both social and monetary outcomes in a similar way. To our knowledge, no prior study has investigated sex differences in the neural processes underlying consumption of monetary and social reward during adolescence. However, our findings of a relative processing bias in males toward monetary outcomes at the expense of social outcomes is in line with a growing body of literature in adults showing

attenuated interest and (neural) responses in men compared with women to a number of social stimuli, including facial expressions (for recent reviews, see Pavlova, 2017; Proverbio, 2017). For example, men have been reported to find facial expressions less arousing than do women (Proverbio, 2017), and their attention is less biased toward faces relative to women (Pavlova, Scheffler, & Sokolov, 2015), suggesting that these kinds of social stimuli are less salient for males. This lower salience might reflect a relatively reduced motivational significance of facial compared with monetary outcome signals when both are applied in the framework of the delayed incentive task.

Furthermore, we found that boys showed a larger fP3 in the reward compared with the punishment conditions, while no differences between the conditions were observed in girls. This indicates that male adolescents perceive punishment-related outcomes as less salient than reward-related outcomes. It should be stressed that the differential result pattern emerged for the reward versus punishment condition independent of whether a negative or a positive outcome was presented. This suggests that the motivational state of participants (reward vs. punishment orientation) is predominantly relevant for the observed findings. The relatively reduced neural reactivity of boys to punishment fits well with our finding of their slightly lowered BIS scores compared with girls, indicating a somewhat reduced tendency toward punishment-related behaviors often seen in boys (see Paglaccio et al., 2016, for similar results). On the other hand, the relatively enhanced brain reactivity to rewards in adolescent boys is consistent with findings from a recent fMRI study showing a hyperactivation of reward-related brain regions (including the nucleus accumbens) in male adolescents for monetary rewards (Alarcon, Cservenka, & Nagel, 2017). Furthermore, it fits with findings on a later maturation of the medial prefrontal cortex in adolescent boys compared with their female counterparts. The medial prefrontal cortex forms a major part of the mesocorticolimbic dopaminergic pathway, which regulates the incentive salience of rewards through the release of dopamine into the nucleus accumbens (Berridge & Kringelbach, 2015; Walker et al., 2017). Adolescent boys might attribute more salience to rewards because of the less mature mesocorticolimbic dopaminergic pathway and might thus be more prone to engage in risky behaviors to achieve these rewards (Alarcon et al., 2017; Walker et al., 2017).

In future longitudinal studies, it would be an important research goal to examine whether the relatively enhanced neural reward orientation in adolescent boys, as assessed with ERPs, might relate to adverse behaviors (including reckless risk taking), which are more common in males (Shulman, Harden, Chein, & Steinberg, 2015) and which can affect mental well-being.

In regard of the FRN, amplitudes in the MR and MP condition in both groups were more pronounced for negative

compared with positive outcomes. This result is in line with studies that have found higher FRN amplitudes to perceived unfavorable compared with favorable outcomes (for a review, see Walsh & Anderson, 2012) and further supports the notion that this component reflects the subjective binary evaluation of an outcome as “good” or “bad” (Hajcak, Moser, Holroyd, & Simons, 2006). It is worth mentioning that the FRN was not reliably elicited in the social conditions. In this context, it should be stressed that this component is typically studied in response to monetary or other nonsocial incentives (e.g., Gehring & Willoughby, 2002; Hajcak, Moser, Holroyd, & Simons, 2007; Holroyd et al., 2006). Notwithstanding this issue, recent research has demonstrated that the FRN is influenced by social contextual factors (Gonzalez-Gadea et al., 2016; Hobson & Inzlicht, 2016) and can also be elicited in response to social incentives (Stavropoulos & Carver, 2014b; Sun & Yu, 2014). One reason the FRN was elicited in the monetary but not in the social conditions might be that the *perceived* difference between a “good” and “bad” outcome was larger in the monetary conditions (thus, a FRN was elicited) but weaker in the social conditions. It is suggested that the social incentive stimuli were not as motivationally relevant as the monetary incentive stimuli. This is supported by the fact that RTs were faster in the monetary than in the social trials across both groups.

In the present study, we did not find sex-related differences in the FRN in the monetary conditions. Previous research yielded inconsistent findings in respect of the FRN: Although some studies reported that adolescent boys (compared with girls) exhibit larger FRN amplitudes (Crowley et al., 2013; Yi et al., 2012) or a stronger modulation of this component dependent on the outcome (Grose-Fifer et al., 2014), findings from other studies contradict these results (e.g., Santesso et al., 2011). Divergent findings between the studies might be related to differences in the experimental paradigms applied as well as in factors known to influence the FRN, including reward probability and action outcome contingencies (Walsh & Anderson, 2012). In future studies, it would be important to address these issues to systematically explore under which conditions sex-related differences in the FRN during adolescence can or cannot be observed.

Limitations and conclusions

A limitation of the present study might be that the affective incentives applied in the social conditions were photographs depicting emotional faces. These stimuli might not be as motivationally relevant as the stimuli in the monetary condition, where participants gained and lost real money. Future studies should address this point by applying social incentives that more closely resemble real-life social feedback (e.g., simulating peer feedback; Spielberg et al., 2015). The present study did not elucidate potential relationships between

pubertal status, puberty hormones, and neurophysiological mechanisms of reward and punishment processing. Cortical changes during adolescence (e.g., in the volume of the medial prefrontal cortex) have been associated with adrenal/gonadal markers of puberty (Walker et al., 2017). Because females go through puberty earlier than males (Sisk & Foster, 2004), these cortical changes are more advanced in adolescent girls than in boys of the same age. The medial prefrontal cortex is a critical part of the dopaminergic pathway and plays an important role in regulating reward-related responses. The earlier maturation of the medial prefrontal cortex in girls due to pubertal hormones might in part explain the reduced reward responsiveness in female compared with male adolescents (Walker et al., 2017). In future ERP investigations, it would be worthwhile to also assess the pubertal status and hormonal indices of puberty to be able to draw a more comprehensive picture. Moreover, as the sample size of the present study was relatively small, and more girls than boys were included, a replication of our findings in a larger and more balanced sample is clearly needed to draw more rigorous conclusions. Because of the limited sample size, we refrained from applying a correction for multiple comparisons for the post hoc *t* tests. In this respect, exploratory analyses revealed that all our findings, except the finding of a reduced SPN in boys in the social punishment condition, would have survived a Bonferroni–Holm correction. However, this analytic approach would have rendered comparison with previous ERP studies more difficult, as most of these studies did not apply a correction for multiple comparisons.

Despite these limitations, to our knowledge, the present study is the first to reveal sex differences in the neurophysiological mechanisms underlying social and monetary incentive processing in adolescence. Our findings demonstrate that adolescent boys and girls show distinct neural patterns during incentive processing, depending on the phase (anticipation vs. consumption), the outcome modality (reward vs. punishment), and the incentive type (social vs. monetary) investigated. The results of the present study highlight the importance of taking sex into account when examining the neurophysiological mechanisms underlying monetary and social incentive processing during adolescence. Future studies should examine the specificity of the findings by including children, adolescents, and adults using the same methodological framework. Moreover, in future longitudinal investigations, it would be important to explore whether the identified sex differences might relate to vulnerabilities of adolescent boys and girls with respect of certain forms of problem behaviors/psychopathology (e.g., risk taking). If such links can be established, neurobiological approaches might prove helpful in identifying individuals who are at increased risk for adverse developmental pathways (see Giedd, 2008). Finally, an important consequence of sex differences in the neural responsiveness to rewards and punishment during adolescence is that

treatments for psychiatric disorders that employ incentives (e.g., cognitive-behavior therapy) might have differential effects in adolescent girls versus boys affected by such disorders (Lenroot & Giedd, 2010). However, in this respect, it would be important to extend the approach of the present investigation to clinical groups to make more far-reaching conclusions.

Acknowledgements We are grateful to all participants with their families who took part in this study. We further would like to thank Carolina Silberbauer and Petra Wagenbüchler for their assistance during data collection. This work was supported by the Faculty of Medicine, University of Munich (Förderprogramm für Forschung und Lehre to E.G; 776).

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