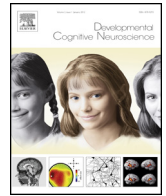




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Anticipatory representations of reward and threat in perceptual areas from preadolescence to late adolescence

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ABSTRACT

This study examined whether changes in perceptual processes can partially account for the increase in reward-orientated behaviour during adolescence. This was investigated by examining reinforcement-dependent potentiation to discriminative stimuli (S^D) that predicted rewarding or threatening outcomes. To that end, perceptual event-related potentials that are modulated by motivationally salient stimuli, the N170 and Late Positive Potential (LPP), were recorded from 30 preadolescents (9–12 years), 30 adolescents (13–17 years), and 34 late adolescents (18–23 years) while they completed an instrumental task in which they emitted or omitted a motor response to obtain rewards and avoid losses. The LPP, but not the N170, showed age, but not gender, differences in reinforcement-dependent potentiation; preadolescents, adolescents, and late adolescents showed potentiation to S^D that predicted a threat, whereas only preadolescents showed potentiation to S^D that predicted a reward. Notably, the magnitude of threat-related LPP reinforcement-dependent potentiation decreased during the course of adolescence. In addition, greater sensation seeking was associated with greater LPP amplitudes in preadolescent males, but smaller LPP amplitudes in late adolescent males. Critically, these findings provide initial evidence for developmental differences in value-related coding in perceptual areas, where adolescents show greater perceptual biases to avoidance-related cues than to reward-related cues.

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1. Introduction

Action selection during adolescence is frequently sub-optimal (Casey et al., 2008; Figner et al., 2009). This promotes potentially harmful risk-taking, often with adverse outcomes for both the individual and society (Steinberg, 2005). It is therefore important to understand the neural mechanisms that underlie suboptimal action selection during adolescence. To that end, this study investigated reinforcement-dependent potentiation in perceptual areas to visual cues that predicted either a rewarding or threatening outcome in an instrumental conditioning task. Reinforcement-dependent potentiation to these cues was indexed by two perceptual event-related potentials (ERPs) that have been reliably implicated in the processing of motivationally salient stimuli, the N170 and Late Positive Potential (LPP) (e.g., Blau et al., 2007; Cuthbert et al., 2000). Moreover, since there are considerable gender differences in brain maturation (DeBellis et al., 2001; Lenroot et al., 2007) and risk-taking behaviours

(Byrnes et al., 1999) throughout adolescence, an exploratory aim of this study was to examine gender-related differences in the reinforcement-dependent modulation of perceptual processes and in how these processes may relate to sensation seeking and risk-taking behaviours during adolescence.

Developmental differences in reinforcement-dependent potentiation, *i.e.*, value-related encoding in perceptual areas, could be an important mechanism underlying increased risk-taking behaviours during adolescence. This is because differences in value-related encoding in perceptual areas could evoke a differential cascade of events important for action selection, preparation, and implementation (Hegd  and Felleman, 2007; Freese and Amaral, 2005; Lamme and Roelfsema, 2000; Lang and Bradley, 2010; Sugase et al., 1999; Vuilleumier, 2005). Consistent with this idea, we recently found that adolescents had greater reinforcement-dependent potentiation of the N170 to visual cues that predicted a threatening outcome compared to young adults (Levita et al., 2015). This finding raised three interesting questions. First, if adolescents show enhanced potentiation of N170 amplitudes to cues that predict threatening outcomes, why are risk-taking behaviours so prevalent during adolescence? Second, how does enhanced N170 potentiation to cues that predict threatening outcomes during adolescence fit with evidence showing that adolescents are highly

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motivated by rewards (e.g., Ernst et al., 2011; Ernst et al., 2006; Steinberg, 2008; Van Leijenhorst et al., 2010)? Third, how does reinforcement-dependent potentiation of ERPs involved in processing rewarding and threatening outcomes change during the course of adolescence? This study was designed to address these questions by examining reinforcement-dependent potentiation of ERPs to visual cues that predicted either a rewarding or threatening outcome during adolescence. Reinforcement-dependent potentiation in the current study was examined using early (N170) and late (LPP) perceptual ERPs that are modulated by motivationally salient stimuli (Levita et al., 2015; Keil et al., 2002; Rellecke et al., 2013; Sabatinelli et al., 2007; Schupp et al., 2000).

The N170 is a negative component that peaks approximately 170 ms post stimulus onset. N170 amplitudes are maximal in occipitotemporal regions, with source localisation studies showing that the N170 indexes activity in the superior temporal sulcus and fusiform gyrus (Sadeh et al., 2010). The N170 reflects early visual processing and has greater amplitudes in response to human faces compared to non-face stimuli (Bentin et al., 1996; Jeffreys, 1989). Conditioned and unconditioned emotional stimuli, including learned danger cues (Dolan et al., 2006; Levita et al., 2015) and emotional facial expressions (Batty and Taylor, 2003; Blau et al., 2007; Mühlberger et al., 2009; Rellecke et al., 2013), also elicit greater N170 amplitudes compared to control stimuli. There is also evidence that other early visual ERPs potentials such as the C1 and early posterior negativity are potentiated to conditioned visual stimuli that predict threatening outcomes, including aversive pictures (Stolarova et al., 2006) and fearful faces (Pizzagalli et al., 2003; Pourtois et al., 2004). Potentiation of early visual components to motivationally salient stimuli is thought to result from re-entrant processing loops between the amygdala and visual cortex (Dolan, 2002; Vuilleumier, 2005). These re-entrant processing loops modulate cortical firing in the visual cortex to increase the processing of salient stimuli (Keil et al., 2009; Sabatinelli et al., 2009) and generate faster responses in potentially threatening situations (Armony and Dolan, 2002; Carlson and Reinke, 2010).

Developmentally, the N170 has been identified in children as young as 4 years old (Batty and Taylor, 2006; Taylor et al., 2001), and N170 amplitudes become more negative in the transition from childhood to adulthood (Batty and Taylor, 2006; Hileman et al., 2011; Taylor et al., 1999). Furthermore, reinforcement-dependent potentiation of the N170 to cues that predict a threatening outcome is greater for adolescents compared to young adults (Levita et al., 2015).

In contrast to the N170, the LPP is a slow, positive component that emerges 300–400 ms post stimulus onset and usually lasts for the duration of the stimulus presentation (Cuthbert et al., 2000). LPP amplitudes are potentiated to positive and negative visual stimuli compared to neutral stimuli (Cuthbert et al., 2000; Schupp et al., 2000; Schupp et al., 2004), and are therefore thought to reflect selective attention to motivationally salient stimuli (Schupp et al., 2006). No study to date has examined the LPP in response to conditioned stimuli. However, there is evidence that the P3b, a late positive component related to the LPP, is potentiated in response to conditioned stimuli that predict rewarding (Broyd et al., 2012; Goldstein et al., 2006; Ramsey and Finn, 1997; Santesso et al., 2012) and threatening (Franken et al., 2011) outcomes. Despite LPP amplitudes being maximal in centroparietal regions, a wide neural network generates the LPP, involving concurrent activity in brain regions associated with visual/attentional processing, including the lateral occipital, parietal and inferotemporal cortices, and emotional processing, including the orbitofrontal cortex, insula, anterior cingulate cortex, ventral striatum and amygdala (Moratti et al., 2011; Liu et al., 2012; Sabatinelli et al., 2007, 2013).

The LPP has also been identified in children as young as 4 years old (Hua et al., 2014). Like adults, children and adolescents

have larger LPP amplitudes for motivationally salient stimuli compared to neutral stimuli (Dennis and Hajcak, 2009; Hajcak and Dennis, 2009; Kujawa et al., 2012; Kujawa et al., 2012, 2013a; Solomon et al., 2012). However, developmental differences have also been observed, with LPP amplitudes decreasing during childhood and adolescence, regardless of the valence of the visual stimulus (Kujawa et al., 2012; MacNamara et al., 2016). In addition, the topography of the LPP changes with age; maximal LPP amplitudes shift from occipitoparietal regions in children and adolescents (Hajcak and Dennis, 2009; Kujawa et al., 2012, 2013b) to more centroparietal regions in adults (Hajcak et al., 2012). The developmental changes in the LPP are consistent with the changes in brain structure, function, and reorganisation during adolescence (Thompson et al., 2000). The human brain matures in a back-to-front fashion, with occipital areas maturing first and prefrontal areas maturing last (Giedd et al., 1999; Petanjek et al., 2011). The prolonged maturation of the prefrontal cortex during adolescence is thought to underlie the changes in LPP amplitude and topography during adolescence, as the LPP appears to be modulated by both 'top-down' prefrontal and 'bottom-up' occipitotemporal areas (Ferrari et al., 2008). Indeed, a broad frontoparietal neural network has been shown to generate and modulate the LPP (Moratti et al., 2011). Therefore, it is possible that the LPP shifts from predominantly occipitoparietal regions to prefrontal-parietal networks as the prefrontal cortex matures during the course of adolescence.

In adulthood, both the N170 (Dolan et al., 2006; Pizzagalli et al., 2003) and LPP (Pastor et al., 2015; Pizzagalli et al., 2003) show reinforcement-dependent potentiation during classical conditioning; larger N170 and LPP amplitudes are elicited by conditioned stimuli that predict the onset of an aversive unconditioned stimulus. However, there is a scarcity of studies examining the reinforcement-dependent potentiation of the N170 and LPP during instrumental tasks, where individuals learn to associate discriminative stimuli (S^D) with a particular response-outcome contingency. To the authors' knowledge, only one study has examined modulation of the N170 in an instrumental task (Levita et al., 2015), and no studies to date have examined modulation of the LPP in an instrumental task, with most studies examining the LPP using passive viewing paradigms (e.g., Cuthbert et al., 2000; Hajcak and Dennis, 2009). Using an instrumental task will enable us to examine the functional significance of N170 and LPP activity in response to reward-related and avoidance-related cues, and their possible role in guiding appropriate action-outcome behaviours.

To that end, we designed an instrumental conditioning task based on a validated avoidance paradigm that has been used in a developmental EEG study and adult fMRI study (Levita et al., 2012, 2015). In this task, participants learned to emit or withhold a motor response to S^D to either obtain a reward (gaining points) or avoid a negative outcome (losing points). Participants also had to emit or withhold a motor response for two control cues, which did not predict the onset of a rewarding or threatening outcome. The control cues allowed us to determine whether developmental changes in the N170 and LPP were due to differences in the potentiation of anticipatory responses to cues that predicted positive or negative outcomes instead of being a result of the developmental differences in motor, motor-preparation, or visual processes associated with an instrumental procedure. Given that the human brain undergoes a protracted development across adolescence (Gogtay et al., 2004; Tiemeier et al., 2010), participants aged 9–23 years old took part in this study. Participants were split into three age groups: preadolescents aged 9–12 years; adolescents aged 13–17 years; and late adolescents aged 18–23 years. Preadolescence reflects the developmental stage occurring between childhood and adolescence, while late adolescence reflects the transition from adolescence into young adulthood. Adolescence is not an isolated period in development, but a transitional phase that bridges the gap between childhood and

adulthood. Thus, examining the transitions into and out of adolescence is crucial for understanding the discrete changes that occur during adolescence (Casey et al., 2008).

The main aim of this study was to examine age- and gender-related effects in the potentiation of N170 and LPP amplitudes to visual cues that predict either a rewarding or threatening outcome compared to control stimuli. Based on the research discussed, it was predicted that: (a) N170 and LPP amplitudes would show reinforcement-dependent potentiation to visual cues that predict either rewarding or threatening outcomes compared to control cues, and that reinforcement-dependent potentiation of the N170 and LPP would be greater in adolescents compared to preadolescents and late adolescents; (b) irrespective of condition, N170 and LPP amplitudes would decrease from preadolescence to late adolescence; (c) females would show greater N170 and LPP reinforcement-dependent potentiation compared to males. This study also had two exploratory aims. First, this study aimed to examine the functional significance of reinforcement-dependent potentiation during adolescence by assessing the relationships between participants' reaction times and ERP amplitudes. It was predicted that reaction times would be negatively associated with N170 and LPP potentiation. Second, this study aimed to assess whether value-related encoding in perceptual areas is associated with risk-taking behaviours and sensation seeking. It was expected that greater risk-taking behaviours and sensation seeking would be associated with greater N170 and LPP amplitudes. Since adolescent males take significantly more risks than adolescent females (Byrnes et al., 1999), it was expected that these relationships would be particularly prominent for males.

2. Method

2.1. Participants

Ninety-five volunteers aged 9–23 years old participated in this study. One participant was excluded due to excessive EEG artefacts. Participant demographics for the final sample are displayed in Table 1. Participants were split into three age groups: preadolescents aged 9–12 years; adolescents aged 13–17 years; and late adolescents aged 18–23 years. All participants were right-handed, native English speakers, had normal or corrected-to-normal vision, normal hearing, and no current neurological, psychiatric, or medical conditions. Handedness was measured using the Edinburgh Handedness Inventory (Oldfield, 1971). A *Gender* (females vs males) by *Age Group* (preadolescents vs adolescents vs late adolescents) ANOVA found no significant differences in handedness between groups ($p > 0.05$). Participants were recruited through the University of Sheffield and local advertising. Full, informed consent was received from all participants, as well as from a parent or guardian of all participants under the age of 18 years. All participants received £10 for taking part. The study was approved by the Department of Psychology, University of Sheffield Ethics Committee.

Table 1
Participant demographics.

Age Group	Gender	n	Age M (SD)	BSSS M [95% CI]	YRBSS M [95% CI]
Preadolescents 9–12 years	Females	15	10.80 (1.26)	26.73 [23.72, 29.75]	0.53 [0.12, 0.94]
	Males	15	10.53 (1.30)	26.93 [24.70, 29.16]	0.93 [0.32, 1.54]
Adolescents 13–17 years	Females	15	14.67 (1.59)	30.33 [27.90, 32.76]	1.87 [1.03, 2.70]
	Males	15	14.80 (1.42)	26.67 [23.24, 30.10]	4.00 [2.61, 5.39]
Late Adolescents 18–23 years	Females	18	20.39 (1.38)	28.78 [25.89, 31.67]	4.22 [3.25, 5.20]
	Males	16	21.00 (1.55)	26.69 [23.92, 29.45]	3.25 [2.07, 4.43]

Note: BSSS = Brief Sensation Seeking Scale; YRBSS = Youth Risk Behaviour Surveillance Survey.

2.2. Apparatus

The task was delivered using a Viglen Intel Pentium 4 3 GHz computer and presented on a Viglen Omnino III monitor with a 1024 × 768 pixel resolution and 60 Hz refresh rate. The visual stimuli used in the task were created by Scott Yu and provided by Michael J. Tarr for the Neural Basis of Cognition and Department of Psychology, Carnegie Mellon University (<http://www.tarrlab.org>). Since the N170 ERP is sensitive to the low-level visual properties of stimuli (Eimer, 2011; Rossion and Caharel, 2011), the visual stimuli used in this task were matched for orientation, luminosity, and contrast, and counterbalanced across participants. Visual stimuli were presented on a black background, and motor responses to the visual stimuli were collected using the space bar. Matlab v2012a was used to program and deliver the task. For the duration of the task, participants were seated approximately 70 cm away from the computer monitor in a dimly lit room shielded by a Faraday cage.

2.3. Instrumental conditioning task

The instrumental conditioning task used in this study was an extension of a validated avoidance paradigm previously used in a developmental EEG study and fMRI study in adults (Levita et al., 2012, 2015). Participants completed the task while having their brain activity measured using EEG. The task was composed of a reward block and an avoidance block. Both the reward and avoidance blocks included two S^D and two control stimuli. The S^D predicted a positive outcome (winning 10 points) in the reward block and a negative outcome (losing 10 points) in the avoidance block. In the reward block, one of S^D required participants to emit an action to win 10 points (Reward^{Go}; RG; Fig. 1a), while the other S^D required participants to withhold an action to win 10 points (Reward^{NoGo}; RN; Fig. 1b). Participants only won points for a trial if they made the correct motor response. In order to increase the potential threat associated with losing points, the reward block always occurred before the avoidance block. In the avoidance block, one of the S^D required participants to emit an action to avoid losing 10 points (Avoidance^{Go}; AG; Fig. 1c), while the other S^D required participants to withhold an action to avoid losing 10 points (Avoidance^{NoGo}; AN; Fig. 1d). Participants lost 10 points for each incorrect response. The two control stimuli were consistent across the reward and avoidance blocks. Participants were required to emit an action for one of the control stimuli (Control^{Go}; CG; Fig. 1e), and withhold an action for the other control stimulus (Control^{NoGo}; CN; Fig. 1f). Participants were told that the control cues were not associated with a positive or negative outcome, but were included to ensure they were paying attention throughout the task. The control stimuli provided comparison conditions to examine reinforcement-dependent potentiation to the S^D . For both the S^D and control stimuli, participants were told to emit or withhold their motor response while the yellow cross was displayed on the screen. This allowed us to separate out anticipatory representations of positive and negative outcomes from motor responses. For the S^D only, participants received feedback about their response in order

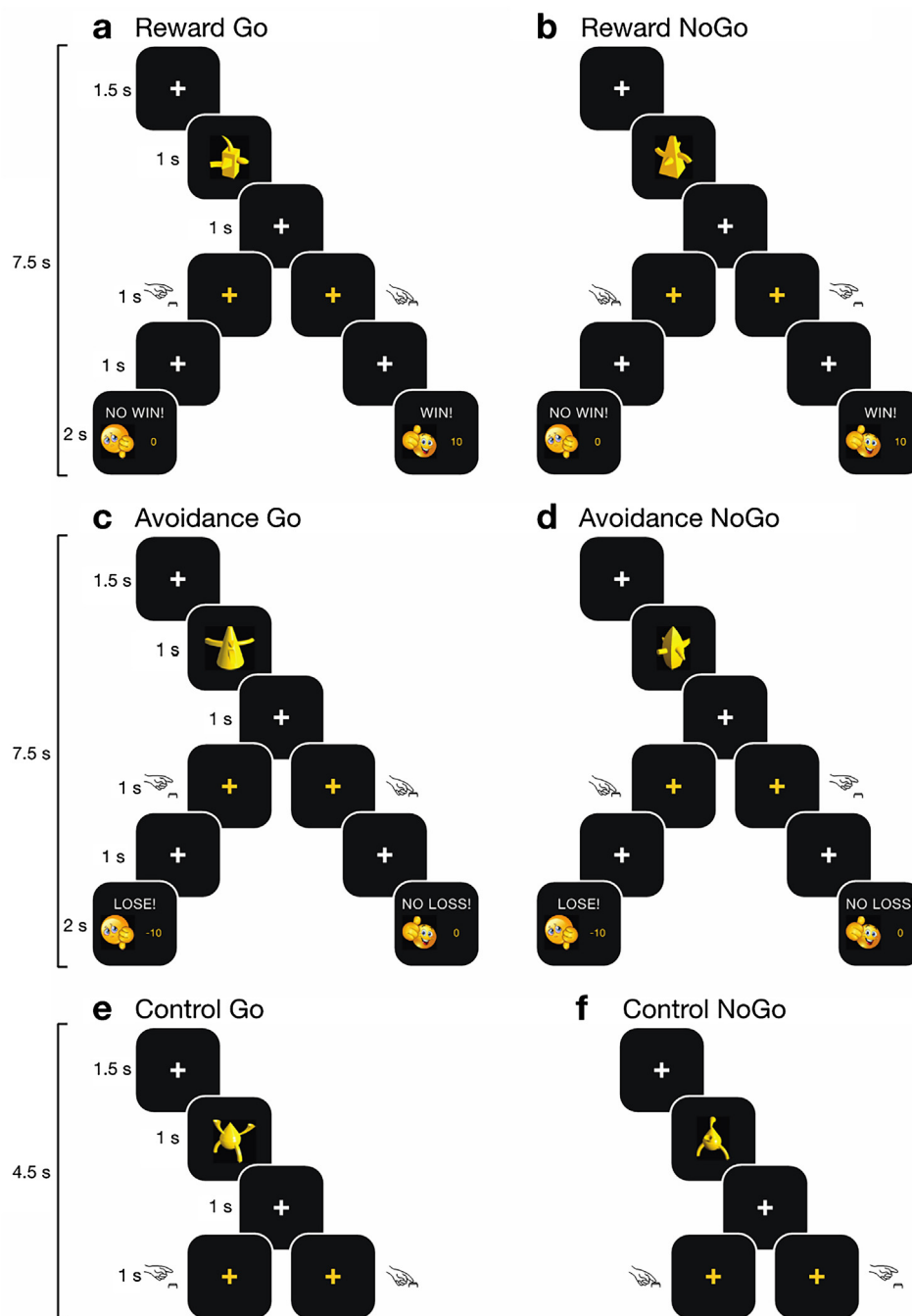


Fig. 1. The instrumental task was composed of a reward block (a, b, e, f) and avoidance block (c, d, e, f). Both the reward and avoidance blocks included two discriminative stimuli (S^D) (a, b, c, d) and two control stimuli (e, f). The S^D predicted a positive outcome (winning 10 points) in the reward block and a negative outcome (losing 10 points) in the avoidance block. For all conditions, participants were presented with a white fixation cross, followed by the visual cue. Participants were required to wait until the yellow fixation cross appeared on the screen before emitting or withholding their motor response. For S^D , participants saw one of two feedback screens indicating whether or not they had made the correct response. For control cues, participants received no feedback since control cues were not associated with a positive or negative outcome.

to reinforce the correct response-outcome contingency. The feedback included whether they had made the correct motor response and their current total points score. There were 72 presentations of each stimulus in both the reward and avoidance blocks. The stimuli were presented in a pseudorandom order, with the same stimulus not being presented more than twice consecutively. Each block was split into four 8-minute sections to allow participants to take regular breaks.

In order to try and minimise potential age-dependent differences in task performance, participants had to complete a set of

practice trials before the start of each block. To ensure participants had learned the task contingences, participants had to get 75 per cent of the practice trials correct and verbally recall the correct response to each stimulus.

2.4. EEG recording and preprocessing

EEG signals were recorded using Biosemi Active Two 64 channel+CMS/DRL electrode caps, and Biosemi 'Pin-Type' Ag-AgCl active electrodes. The electrode caps were fitted according to the

10/20 electrode system. Four Biosemi flat active electrodes placed on participants' temples, and above and below their left eye, were used to monitor participants' eye movements, allowing for the detection of ocular artefacts. EEG and EOG signals were amplified using the Biosemi ActiveTwo AD-Box. Electrode offsets were kept below ± 25 Hz. The EEG was recorded continuously with a sampling rate of 2048 Hz.

All EEG preprocessing was conducted offline. EEG data were decimated from 2048 to 512 Hz using Biosemi's decimator software. Trials with incorrect behavioural responses were not included in the EEG analysis. EEG data were imported into EEGLAB v13.5.4b (Delorme and Makeig, 2004) using Cz (the vertex) as the reference electrode. ERPLAB v5.0 (Lopez-Calderon and Luck, 2014) was used to band-pass filter the continuous EEG data between 0.1–30 Hz and remove the direct current offset. EEGLAB was used for the subsequent analyses. Trials were split into -200 to 800 ms epochs relative to the stimulus onset, and bad channels were visually identified and rejected. An Independent Components Analysis (ICA) was conducted to identify and correct vertical and horizontal ocular movements. Prior to running the ICA, trials with eye blinks occurring within 200 ms of the stimulus onset were rejected to ensure that participants had seen the visual stimulus. Following ocular artefact correction, rejected bad channels were interpolated and epochs were baseline corrected. To remove additional artefacts in the data, epochs with amplitude differences larger than $\pm 150 \mu\text{V}$ were rejected. All participants had a minimum of 25 epochs following artefact rejection. Finally, trials within each condition were averaged to create grand average ERP waveforms for each group.

To reduce the number of statistical comparisons, electrodes were clustered on the basis of the topographical maps. The N170 was identified at O1, PO3, and PO7 in the left hemisphere, and O2, PO4, and PO8 in the right hemisphere. Selecting both right and left hemisphere electrode clusters for the N170 provided a way to assess laterality effects. The LPP was identified at central occipitoparietal electrodes and therefore Pz, P1, P2, and POz were clustered for LPP analyses. Time windows of 150–220 ms and 400–700 ms were selected for the N170 and LPP, respectively. Rectified area under the curve within each time window was used to quantify ERP amplitudes.

2.5. Sensation seeking and risk-taking behaviours

An exploratory aim of this study was to examine whether value-related encoding in perceptual areas is associated with increases in risk-taking behaviours and sensation seeking during adolescence. Sensation seeking was measured using the Brief Sensation Seeking Scale (BSSS; Hoyle et al., 2002). The BSSS is a short 8-item scale. Responses are collected on a five-point Likert scale and summed together to create a total score (maximum score of 40). Greater scores indicate a greater propensity for sensation seeking. Risk-taking behaviours were measured using the Youth Risk Behaviour Surveillance Survey (YRBSS; Centers for Disease Control and Preventions, 2001). A 10-item version of the YRBSS was administered to all participants (Aklin et al., 2005). Participants indicated whether or not they had engaged in the following behaviours during the previous twelve months: drunk alcohol; smoked a cigarette; used any illegal drug; gambled for real money; had sexual intercourse without a condom; stolen anything from a store; carried a weapon outside of their home; been in a physical fight; ridden in a car without a seatbelt; ridden a bicycle or motorcycle without wearing a helmet. Responses were coded 1 for yes and 0 for no, and summed together to compute a total score (maximum score of 10). Greater scores reflect a greater engagement with real world risk-taking during the previous twelve months.

2.6. Statistical analyses

Behavioural and ERP data were analysed using IBM SPSS statistics v22.0. The significance level was set at $p < 0.05$ for all analyses.

3. Results

3.1. Task performance

Task performance was indexed using accuracy and reaction time. Accuracy scores reflect the percentage of correct responses for each condition. Reaction times were measured for conditions that required a motor response (Reward^{Go}, Avoidance^{Go}, Control^{Go}), and reflect the time it took for participants to make a motor response while the yellow fixation cross was displayed on the screen. Only trials with correct behavioural responses were included in the reaction time analyses.

3.1.1. Accuracy

Supplementary Table 1 displays the means and confidence intervals for task accuracy. To assess age- and gender-related differences in task accuracy, two mixed-design ANOVAs were conducted with *Condition* (S^D (Reward^{Go} and Reward^{NoGo}/Avoidance^{Go} and Avoidance^{NoGo}) vs control (Control^{Go} and Control^{NoGo})) and *Action* (motor action (Reward^{Go}/Avoidance^{Go} and Control^{Go}) vs no motor action (Reward^{NoGo}/Avoidance^{NoGo} and Control^{NoGo})) as the within-group factors, and *Gender* (females vs males) and *Age Group* (preadolescents vs adolescents vs late adolescents) as the between-group factors. Separate ANOVAs were conducted for the reward and avoidance blocks.

Task accuracy was very high, with all groups responding correctly to at least 85 per cent of trials for all conditions. Despite this, the ANOVAs revealed small, but significant, differences between conditions and age groups for the reward and avoidance blocks. For both the reward and avoidance blocks, main effects of *Age Group* (reward: $F(2, 88) = 12.24, p < 0.001, \eta_p^2 = 0.28$; avoidance: $F(2, 88) = 14.50, p < 0.001, \eta_p^2 = 0.25$), *Action* (reward: $F(1, 88) = 38.83, p < 0.001, \eta_p^2 = 0.31$; avoidance: $F(1, 88) = 47.53, p < 0.001, \eta_p^2 = 0.35$), and *Condition* (reward: $F(1, 88) = 16.10, p < 0.001, \eta_p^2 = 0.16$; avoidance: $F(1, 88) = 28.13, p < 0.001, \eta_p^2 = 0.24$) were found. Together, these findings show that preadolescents made significantly more errors in both the reward and avoidance blocks compared to adolescents and late adolescents. Moreover, all groups made significantly more errors in response to conditions that required a motor response (Reward^{Go}, Avoidance^{Go}, Control^{Go}) in comparison to conditions that required inhibition of a motor response (Reward^{NoGo}, Avoidance^{NoGo}, Control^{NoGo}). Finally, these findings reveal that all groups made more errors in response to control stimuli (Control^{Go}, Control^{NoGo}) than to S^D (Reward^{Go}, Reward^{NoGo}, Avoidance^{Go}, Avoidance^{NoGo}). No gender differences were observed in task accuracy.

3.1.2. Reaction time

Supplementary Table 2 displays the means and confidence intervals for task reaction time. Age- and gender-related differences in reaction time were also assessed using two mixed-design ANOVAs with *Condition* (S^D (Reward^{Go}/Avoidance^{Go}) vs control (Control^{Go})) as the within-group factor, and *Gender* (females vs males) and *Age Group* (preadolescents vs adolescents vs late adolescents) as the between-group factors. Separate ANOVAs were conducted for the reward and avoidance blocks. No main or interaction effects were found for reaction times for either the reward or avoidance block, indicating that reaction times were equivalent across age groups and genders.

3.2. Event-related potentials

3.2.1. N170 scalp topography

The N170 topographical maps are displayed in Fig. 2. Consistent with the N170 literature (Levita et al., 2015; Rossion et al., 2000), the N170 topographical maps revealed maximal activity in occipitotemporal regions. Developmental patterns were also observed, with neural activity in occipitotemporal regions decreasing across adolescence. There were similar patterns of neural activity for S^D and control stimuli, with the difference maps revealing minimal differences between conditions.

3.2.2. N170 amplitude

Grand average waveforms and group means for the N170 are displayed in Fig. 2. Age- and gender-related differences in N170 amplitudes were assessed using mixed-design ANOVAs, with *Condition* (S^D (Reward^{Go} and Reward^{NoGo}/Avoidance^{Go} and Avoidance^{NoGo}) vs control (Control^{Go} and Control^{NoGo})), *Action* (motor action (Reward^{Go}/Avoidance^{Go} and Control^{Go}) vs no motor action (Reward^{NoGo}/Avoidance^{NoGo} and Control^{NoGo})) and *Laterality* (left hemisphere vs right hemisphere) as the within-group factors, and *Gender* (females vs males) and *Age Group* (preadolescents vs adolescents vs late adolescents) as the between-group factors. Since the reward block always preceded the avoidance block, separate ANOVAs were conducted for the reward and avoidance blocks to account for potential time effects. The main effect of *Age Group* was significant for the reward block ($F(2, 88) = 12.80, p < 0.001, \eta_p^2 = 0.23$) and the avoidance block ($F(2, 88) = 8.27, p < 0.001, \eta_p^2 = 0.16$). For the reward block, preadolescents had greater N170 amplitudes ($M = 307.80, 95\% \text{ CI } [265.72, 349.88]$) compared to both adolescents ($M = 203.37, 95\% \text{ CI } [161.29, 245.45]$) ($p = 0.001$) and late adolescents ($M = 164.23, 95\% \text{ CI } [124.63, 203.83]$) ($p < 0.001$). No difference was found between adolescents and late adolescents for N170 amplitudes in the reward block ($p = 0.182$). Similarly, for the avoidance block, preadolescents had greater N170 amplitudes ($M = 285.46, 95\% \text{ CI } [240.99, 329.93]$) compared to both adolescents ($M = 206.45, 95\% \text{ CI } [161.98, 250.92]$) ($p = 0.014$) and late adolescents ($M = 161.44, 95\% \text{ CI } [119.60, 203.28]$) ($p < 0.001$). No difference was found between adolescents and late adolescents for N170 amplitudes in the avoidance block ($p = 0.146$). These findings reveal that N170 amplitudes decreased from preadolescence to adolescence in both the reward and avoidance blocks. No main effects of *Condition* or *Gender* were found for either the reward and avoidance blocks. Moreover, no interactions were found for either the reward or avoidance blocks. Overall, these findings indicate that the N170 was not potentiated by visual cues predicting either a reward or threat.

In order to assess the influence of task performance on N170 amplitudes, the ANOVAs were recomputed with participants' task accuracy scores included as covariates. The main effect of *Age Group* was maintained in the reward block ($F(2, 84) = 10.77, p < 0.001, \eta_p^2 = 0.20$) and avoidance block ($F(2, 84) = 6.50, p = 0.002, \eta_p^2 = 0.13$), and no other main or interaction effects were found after controlling for task accuracy. Hence, task accuracy did not have a significant influence on N170 amplitudes.

3.2.3. LPP scalp topography

LPP topographical maps are displayed in Fig. 3. In accordance with previous work (Dennis and Hajcak, 2009; Hajcak and Dennis, 2009; Kujawa et al., 2012, 2013a, 2013b; Solomon et al., 2012), the LPP scalp topography maps revealed maximal activations over central occipitoparietal regions for all groups. Developmental effects were also observed, with neural activity reducing in magnitude and becoming more focal in centroparietal regions during late adolescence.

3.2.4. LPP amplitude

Grand average waveforms and group means for the LPP are displayed in Fig. 3. Age- and gender-related effects in LPP amplitudes were investigated using mixed-design ANOVAs, with *Condition* (S^D (Reward^{Go} and Reward^{NoGo}/Avoidance^{Go} and Avoidance^{NoGo}) vs control (Control^{Go} and Control^{NoGo})) and *Action* (motor action (Reward^{Go}/Avoidance^{Go} and Control^{Go}) vs no motor action (Reward^{NoGo}/Avoidance^{NoGo} and Control^{NoGo})) as the within-group factors, and *Gender* (females vs males) and *Age Group* (preadolescents vs adolescents vs late adolescents) as the between-group factors. As with the N170, separate ANOVAs were conducted for the reward and avoidance blocks to account for potential time effects.

For the reward block, a main effect of *Condition* was found ($F(1, 88) = 16.69, p < 0.001, \eta_p^2 = 0.16$), revealing that LPP amplitudes were significantly greater for S^D ($M = 944.68, 95\% \text{ CI } [843.25, 1046.12]$) than control stimuli ($M = 823.50, 95\% \text{ CI } [735.03, 911.97]$). A main effect of *Action* was also found ($F(1, 88) = 18.28, p < 0.001, \eta_p^2 = 0.17$), revealing that stimuli requiring a motor response ($M = 953.34, 95\% \text{ CI } [852.26, 1054.43]$) elicited larger LPP amplitudes than stimuli requiring inhibition of a motor response ($M = 814.84, 95\% \text{ CI } [724.10, 905.57]$). A main effect of *Age Group* was also found for the reward block ($F(2, 88) = 18.78, p < 0.001, \eta_p^2 = 0.30$). Planned comparisons showed that preadolescents had greater LPP amplitudes ($M = 1248.45, 95\% \text{ CI } [1088.62, 1408.27]$) compared to both adolescents ($M = 828.26, 95\% \text{ CI } [668.44, 988.09]$) ($p < 0.001$) and late adolescents ($M = 575.56, 95\% \text{ CI } [425.18, 725.95]$) ($p < 0.001$). Adolescents also had greater LPP amplitudes compared to late adolescents ($p = 0.025$), revealing that LPP amplitudes decreased from preadolescence to late adolescence in the reward block.

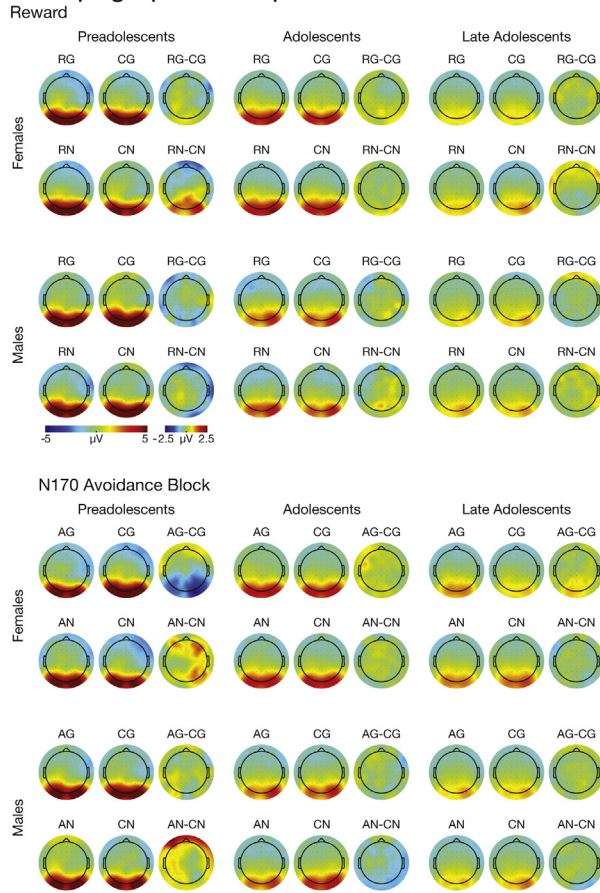
Finally, a *Condition* by *Age Group* interaction was found for the reward block ($F(2, 88) = 4.10, p = 0.020, \eta_p^2 = 0.08$). To examine this interaction, a repeated measures ANOVA was conducted for each age group with *Condition* as the within-group factor. A main effect of *Condition* was found for preadolescents ($F(1, 29) = 13.45, p = 0.001, \eta_p^2 = 0.32$), revealing that LPP amplitudes were significantly greater for S^D ($M = 1369.43, 95\% \text{ CI } [1143.08, 1595.78]$) than control stimuli ($M = 1127.46, 95\% \text{ CI } [903.09, 1351.84]$). In contrast, no main effect of *Condition* was found for adolescents ($F(1, 29) = 3.21, p = 0.084, \eta_p^2 = 0.10$) or late adolescents ($F(1, 33) = 1.19, p = 0.283, \eta_p^2 = 0.04$).

For the avoidance block, a main effect of *Condition* was found ($F(1, 88) = 29.75, p < 0.001, \eta_p^2 = 0.25$), revealing that LPP amplitudes were significantly greater for S^D ($M = 978.15, 95\% \text{ CI } [857.74, 1098.55]$) than control stimuli ($M = 806.02, 95\% \text{ CI } [723.90, 888.14]$). A main effect of *Action* was also found ($F(1, 88) = 104.46, p < 0.001, \eta_p^2 = 0.54$), revealing that stimuli requiring a motor response ($M = 1037.39, 95\% \text{ CI } [928.46, 1146.31]$) elicited larger LPP amplitudes than stimuli requiring inhibition of a motor response ($M = 746.78, 95\% \text{ CI } [651.88, 841.68]$). A main effect of *Age Group* was also found for the avoidance block ($F(2, 88) = 12.86, p < 0.001, \eta_p^2 = 0.23$). Planned comparisons revealed that preadolescents had greater LPP amplitudes ($M = 1211.78, 95\% \text{ CI } [1038.40, 1385.16]$) compared to adolescents ($M = 859.17, 95\% \text{ CI } [685.80, 1032.55]$) ($p = 0.005$) and late adolescents ($M = 605.30, 95\% \text{ CI } [442.16, 768.44]$) ($p < 0.001$). Adolescents also had greater LPP amplitudes compared to late adolescents ($p = 0.037$), showing that LPP amplitudes decreased from preadolescence to late adolescence in the avoidance block.

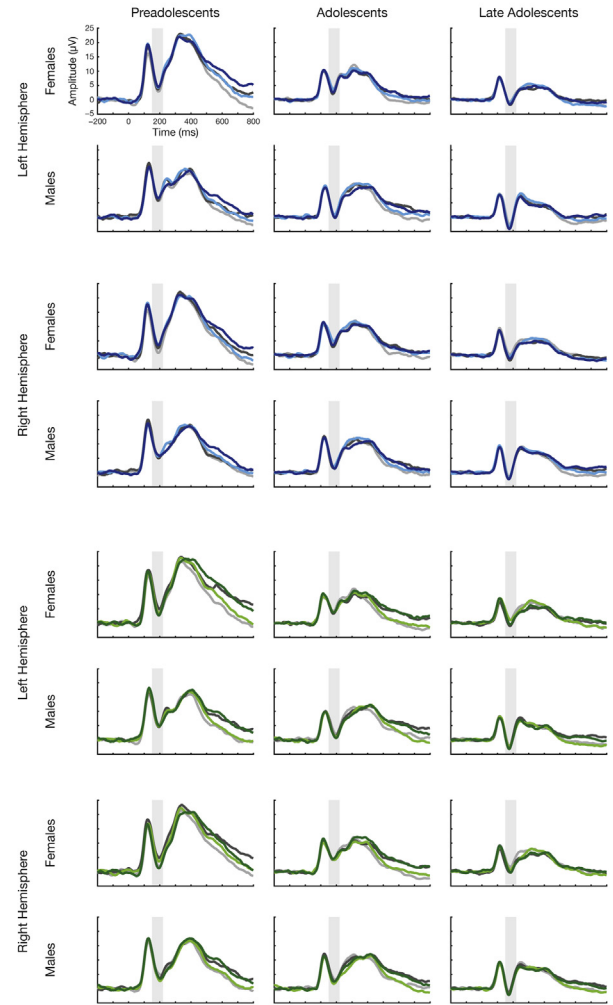
As with the reward block, a *Condition* by *Age Group* interaction was found for the avoidance block ($F(2, 88) = 3.29, p = 0.042, \eta_p^2 = 0.07$). To examine this interaction, a repeated measures ANOVA was conducted for each age group with *Condition* as the within-group factor. A main effect of *Condition* was found for preadolescents ($F(1, 29) = 12.86, p < 0.001, \eta_p^2 = 0.31$), adolescents ($F(1, 29) = 13.34, p < 0.001, \eta_p^2 = 0.32$) and late adolescents ($F(1,$

N170

a Topographical maps



b Waveforms



c Bar graphs

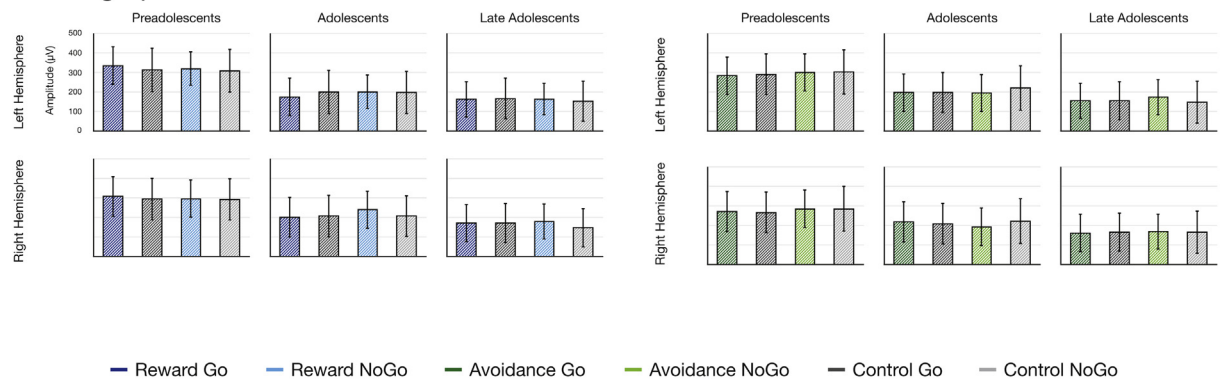


Fig. 2. (a) Scalp topography of the N170 (170–220 ms) for the reward and avoidance blocks. Topographical maps are shown for the S^D and control stimuli, as well as for the differences in activity between S^D and their respective control condition. RG = Reward^{Go}; RN = Reward^{NoGo}; AG = Avoidance^{Go}; AN = Avoidance^{NoGo}; CG = Control^{Go}; CN = Control^{NoGo}. (b) Grand average ERP waveforms at the left and right occipito-temporal electrode clusters for the reward and avoidance blocks. The N170 was identified between 170 and 220 ms post stimulus onset, and is illustrated by the grey area on the graphs. (c) Group means of the N170 at the left and right occipito-temporal electrode clusters for the reward and avoidance blocks. Error bars represent 95% confidence intervals.

33) = 5.17, $p = 0.030$, $\eta_p^2 = 0.14$). These ANOVAs revealed that for all age groups, LPP amplitudes were greater in response to S^D (preadolescents: $M = 1350.53$, 95% CI [1040.66, 1660.39]; adolescents:

$M = 937.52$, 95% CI [771.94, 1103.10]; late adolescents: $M = 650.91$, 95% CI [513.61, 788.21]) than to control stimuli (preadolescents: $M = 1073.03$, 95% CI [871.38, 1274.68]; adolescents: $M = 780.83$, 95%

Late Positive Potential

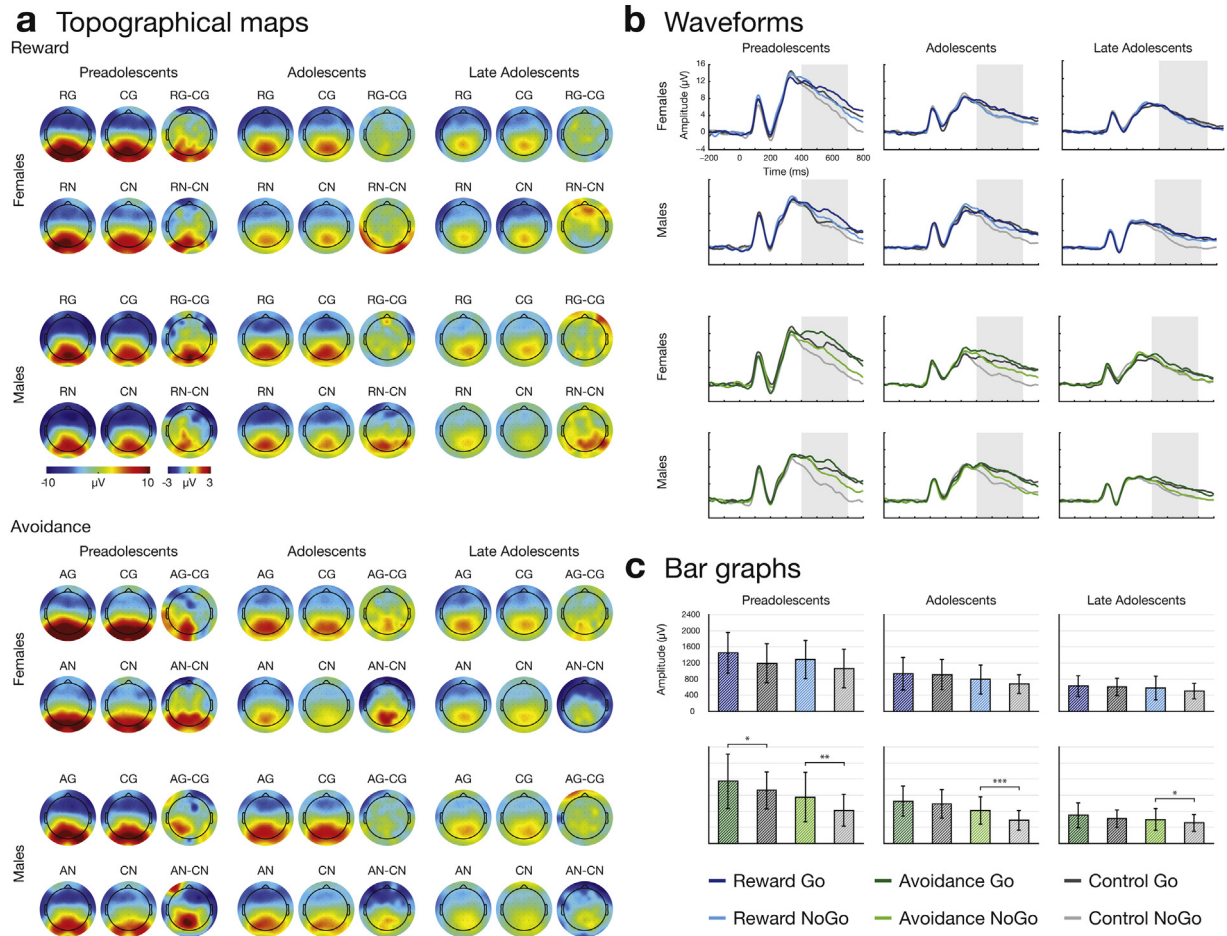


Fig. 3. (a) Scalp topography of the LPP (400–700 ms) for the reward and avoidance blocks. Topographical maps are shown for the S^D and control stimuli, as well as for the differences in activity between S^D and their respective control condition. RG = Reward^{Go}; RN = Reward^{NoGo}; AG = Avoidance^{Go}; AN = Avoidance^{NoGo}; CG = Control^{Go}; CN = Control^{NoGo}. (b) Grand average ERP waveforms at the parietal electrode cluster for the reward and avoidance blocks. The LPP was identified between 400 and 700 ms post stimulus onset, and is illustrated by the grey area on the graphs. (c) Group means of the LPP at the parietal electrode cluster for the reward and avoidance blocks. The significant *Condition* by *Age Group* interactions for the reward and avoidance blocks are indicated on the graphs (the interactions collapsed across Go and NoGo conditions for the S^D and control stimuli). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars represent 95% confidence intervals.

CI [646.50, 915.16]; late adolescents: $M = 566.63$, 95% CI [471.02, 662.24]).

Finally, an *Action* by *Age Group* interaction was found ($F(2, 88) = 12.32$, $p < 0.001$, $\eta_p^2 = 0.22$). To examine this interaction, a repeated measures ANOVA was conducted for each age group with *Action* as the within-group factor. A main effect of *Action* was found for preadolescents ($F(1, 29) = 57.12$, $p < 0.001$, $\eta_p^2 = 0.66$), adolescents ($F(1, 29) = 34.16$, $p < 0.001$, $\eta_p^2 = 0.54$) and late adolescents ($F(1, 33) = 8.51$, $p = 0.006$, $\eta_p^2 = 0.21$), revealing that for all age groups, LPP amplitudes were greater in response to stimuli requiring a motor response (preadolescents: $M = 1433.89$, 95% CI [1162.30, 1705.47]; adolescents: $M = 1019.19$, 95% CI [848.44, 1189.95]; late adolescents: $M = 660.49$, 95% CI [538.94, 782.04]) than to stimuli requiring inhibition of a motor response (preadolescents: $M = 989.67$, 95% CI [749.62, 1229.72]; adolescents: $M = 699.15$, 95% CI [562.31, 836.00]; late adolescents: $M = 557.05$, 95% CI [443.15, 670.96]).

As with the N170, LPP ANOVAs were recomputed with participants' task accuracy scores included as covariates in order to assess the influence of task accuracy on LPP activity. The main effect of *Age Group* was maintained for both the reward block ($F(2, 84) = 10.25$, $p < 0.001$, $\eta_p^2 = 0.20$) and avoidance block ($F(2, 84) = 12.51$, $p < 0.001$, $\eta_p^2 = 0.23$). Moreover, the *Condition* by *Age*

Group ($F(2, 84) = 3.57$, $p = 0.033$, $\eta_p^2 = 0.08$) and *Action* by *Age Group* ($F(1, 84) = 12.83$, $p < 0.001$, $\eta_p^2 = 0.23$) interactions for the avoidance block remained significant after controlling for task accuracy. However, the *Condition* by *Age Group* interaction for the reward block ($F(2, 84) = 2.55$, $p = 0.084$, $\eta_p^2 = 0.06$), and the main effects of *Condition* and *Action* for the reward (*Condition*: $F(1, 84) = 0.78$, $p = 0.378$, $\eta_p^2 = 0.01$; *Action*: $F(1, 84) = 1.63$, $p = 0.205$, $\eta_p^2 = 0.02$) and avoidance (*Condition*: $F(1, 84) = 0.02$, $p = 0.879$, $\eta_p^2 = 0.00$; *Action*: $F(1, 84) = 1.48$, $p = 0.228$, $\eta_p^2 = 0.02$) blocks became non-significant after controlling for task accuracy. These findings therefore suggest that task performance partially affected the magnitude of the LPP.

To determine whether the amount of reinforcement-dependent potentiation in the reward and avoidance blocks changed throughout adolescence, mixed-design ANOVAs were conducted using LPP difference scores, with *Condition* (Reward^{Go} – Control^{Go} vs Reward^{NoGo} – Control^{NoGo}/Avoidance^{Go} – Control^{Go} vs Avoidance^{NoGo} – Control^{NoGo}) as the within-group factor, and *Gender* (females vs males) and *Age Group* (preadolescents vs adolescents vs late adolescents) as the between-group factors. Separate ANOVAs were conducted for the reward and avoidance blocks. Fig. 4 displays the mean LPP difference scores for the reward (Fig. 4a) and avoidance (Fig. 4b) blocks for each age group. For the reward block, a main effect of *Age Group* was found ($F(2,$

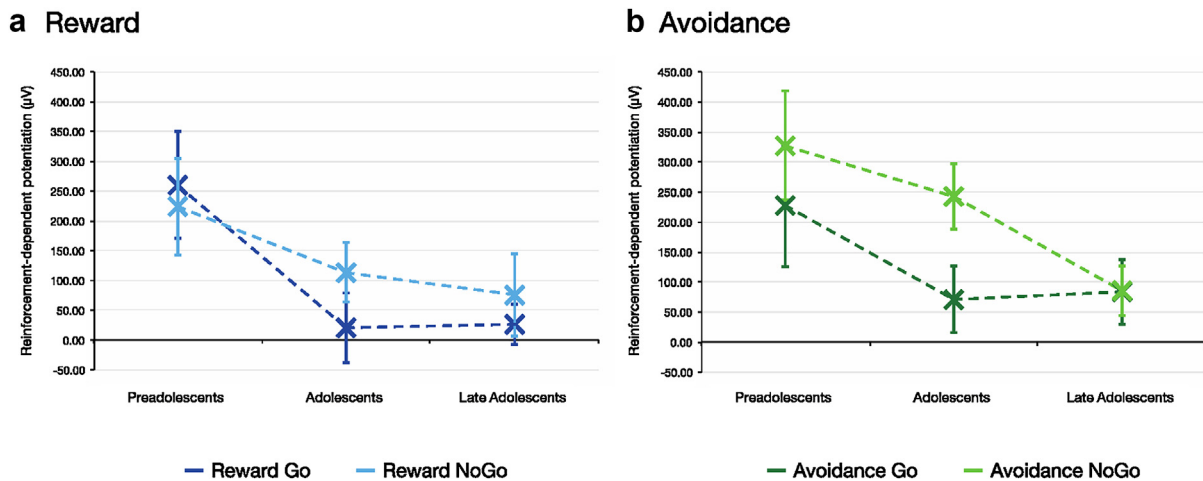


Fig. 4. Group means of LPP reinforcement-dependent potentiation for the reward block (a) and avoidance block (b). LPP reinforcement-dependent potentiation scores were calculated by subtracting control stimuli from their corresponding S^D (Reward^{Go} – Control^{Go}; Reward^{NoGo} – Control^{NoGo}; Avoidance^{Go} – Control^{Go}; Avoidance^{NoGo} – Control^{NoGo}). Error bars represent standard error. LPP reinforcement-dependent potentiation decreased from preadolescence to adolescence in the reward block and from preadolescence to late adolescence in the avoidance block. No significant differences in the developmental trajectories of Go and NoGo cues were found for either the reward or avoidance block.

88) = 4.10, $p = 0.020$, $\eta_p^2 = 0.09$). Planned comparisons revealed that preadolescents ($M = 241.97$, 95% CI [137.87, 346.07]) had greater reinforcement-dependent potentiation than both adolescents ($M = 67.15$, 95% CI [-36.95, 171.44]) ($p = 0.020$) and late adolescents ($M = 54.43$, 95% CI [-43.52, 152.38]) ($p = 0.011$). In contrast, no difference in reinforcement-dependent potentiation was found between adolescents and late adolescents ($p = 0.860$). Similarly, for the avoidance block, a main effect of Age Group was found ($F(2, 88) = 3.29$, $p = 0.042$, $\eta_p^2 = 0.07$). Planned comparisons revealed that preadolescents ($M = 277.50$, 95% CI [166.73, 388.26]) had greater reinforcement-dependent potentiation than late adolescents ($M = 82.19$, 95% CI [-22.04, 186.41]) ($p = 0.012$). However, no significant differences were found between preadolescents and adolescents ($M = 156.69$, 95% CI [45.93, 267.46]) ($p = 0.129$), or between adolescents and late adolescents ($p = 0.333$). Together, these findings suggest that the amount of LPP potentiation decreased from preadolescence to adolescence in the reward block and from preadolescence to late adolescence in the avoidance block. All other main and interaction effects were non-significant.

3.2.5. Summary of ERP findings

No gender differences in N170 or LPP amplitudes were observed for any of the conditions or age groups. However, significant age effects were found in both the reward and avoidance blocks for both the N170 and LPP, with N170 amplitudes decreasing from preadolescence to adolescence, and LPP amplitudes decreasing from preadolescence to late adolescence. Critically, reward- and threat-related potentiation was found for the LPP, but not the N170, whereby greater LPP amplitudes were found in response to S^D compared to control stimuli. Significantly, Condition by Age Group interactions for the reward and avoidance blocks revealed age-dependent differences for LPP potentiation; only preadolescents showed LPP potentiation in the reward block whereas all age groups showed LPP potentiation in the avoidance block. Moreover, the degree of threat-related LPP reinforcement-dependent potentiation decreased from preadolescence to late adolescence, whereas the degree of reward-related LPP reinforcement-dependent potentiation only decreased from preadolescence to adolescence. Finally, in both the reward and avoidance blocks, conditions that required a motor response had larger LPP amplitudes than conditions that required inhibition of a motor response.

3.3. Correlations between LPP amplitude and behavioural measures

Since the N170 was not modulated by S^D that predicted rewarding or threatening outcomes, correlational analyses were limited to LPP amplitudes. Pearson correlation coefficients were used in the correlational analyses. To explore potential age- and gender-related effects, correlations were conducted separately for age groups and genders. All correlational analyses were bootstrapped using bias-corrected and accelerated 95% confidence intervals based on 1000 samples. To correct for multiple comparisons, the Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995) was applied to all correlational analyses with a false discovery rate (FDR) of 0.25. A FDR of 0.25 was selected due to the small sample sizes. As such, the following analyses should be treated as exploratory. The original p values are reported.

3.3.1. Relationships between LPP amplitudes and task reaction time

The first exploratory aim of this study was to examine the functional significance of reinforcement-dependent potentiation by assessing the relationships between participants' reaction times and ERP amplitudes. For the reward block, only one significant positive correlation was found; Reward^{Go} LPP amplitudes were positively correlated to Reward^{Go} reaction times for female adolescents ($r = 0.58$, $p = 0.024$). All other correlations were non-significant. Furthermore, no correlations were found for the avoidance block for any group.

3.3.2. Relationships between LPP amplitudes and measures of risk-taking and sensation seeking

The second exploratory aim of this study was to examine whether value-related encoding in perceptual areas is associated with increases in risk-taking behaviours and sensation seeking during adolescence. No relationships between LPP amplitudes and risk-taking behaviours, as measured by the YRBSS, were found for any group. By comparison, there were age- and gender-related effects for sensation seeking; no correlations between sensation seeking and LPP amplitudes were found for females, whereas there was a strong age-dependent association between sensation seeking and LPP amplitudes for males.

In the reward block, preadolescent males had moderate positive correlations between sensation seeking and LPP amplitudes for Reward^{Go} ($r = 0.59, p = 0.022$), Reward^{NoGo} ($r = 0.55, p = 0.033$), and Control^{NoGo} ($r = 0.53, p = 0.043$). No relationship was found between sensation seeking and LPP amplitudes for Control^{Go} in preadolescent males ($r = 0.38, p = 0.160$). By comparison, no relationships were found between sensation seeking and LPP amplitudes in the reward block for adolescents. However, for late adolescent males, moderate negative correlations were found between sensation seeking and LPP amplitudes for Reward^{Go} ($r = -0.64, p = 0.007$) and Control^{Go} ($r = -0.57, p = 0.022$), but not for Reward^{NoGo} ($r = -0.48, p = 0.058$) or Control^{NoGo} ($r = 0.07, p = 0.793$).

A similar pattern was found for the avoidance block. Preadolescent males showed a positive relationship between sensation seeking and LPP amplitudes for all conditions (Avoidance^{Go}: $r = 0.51, p = 0.051$; Avoidance^{NoGo}: $r = 0.55, p = 0.034$; Control^{Go}: $r = 0.71, p = 0.003$; Control^{NoGo}: $r = 0.63, p = 0.011$). By comparison, no relationships were found between sensation seeking and LPP amplitudes in the avoidance block for adolescents. However, for late adolescent males, only LPP amplitudes for Avoidance^{Go} were negatively associated with sensation seeking ($r = -0.53, p = 0.036$). The relationship between sensation seeking and LPP amplitudes for Control^{Go} was non-significant ($r = -0.37, p = 0.159$), as were the relationships between sensation seeking and LPP amplitudes for Avoidance^{NoGo} ($r = -0.18, p = 0.507$) and Control^{NoGo} ($r = 0.08, p = 0.759$).

4. Discussion

This is the first study to examine developmental changes across adolescence in early occipito-temporal (N170) and late centro-parietal (LPP) ERPs to S^D that predicted either rewarding or threatening outcomes. Contrary to the study predictions, no reinforcement-dependent potentiation of the N170 was found for any age group. In contrast, the LPP showed age-related differences in reinforcement-dependent potentiation; preadolescents, adolescents and late adolescents showed potentiation to S^D that predicted a threat, whereas only preadolescents showed potentiation to S^D that predicted a reward.

4.1. Late positive potential

Classical conditioning studies have shown greater centro-parietal EEG activity in adults for conditioned stimuli compared to unconditioned stimuli (Pastor et al., 2015; Pizzagalli et al., 2003). However, to date, no study has examined how the LPP is modulated in an instrumental conditioning task. Examining LPP modulation in an instrumental task provides a way of assessing the possible role of perceptual processes in action selection. As predicted, and in line with previous classical conditioning studies, LPP amplitudes were potentiated in centro-parietal areas for S^D that predicted a rewarding outcome and for S^D that predicted a threatening outcome relative to control stimuli. Together, these findings support previous developmental and adult studies showing that LPP amplitudes are greater in response to primary reinforcers, such as pleasant and unpleasant pictures, compared to neutral stimuli, in passive picture viewing tasks (e.g., Cuthbert et al., 2000; Hajcak and Dennis, 2009).

Critically, the reinforcement-dependent potentiation of the LPP changed during the course of adolescence. Reward-related LPP potentiation was only observed in preadolescents, whereas all age groups showed threat-related LPP potentiation. These findings suggest that S^D predicting a threatening outcome may have been more salient during adolescence and late adolescence than S^D predicting a rewarding outcome. However, it is important to note that responses to the avoidance S^D changed with age; the magnitude

of LPP reinforcement-dependent potentiation to the threat-related cues decreased with age, with preadolescents showing the highest levels of LPP reinforcement-dependent potentiation compared to the adolescent and late adolescent groups.

Previous studies have reported that the salience of primary and secondary reinforcers, including appetitive and aversive tastes (Galván and McGlennen, 2013) and money (Barkley-Levenson and Galván, 2014), decreases from mid-adolescence to late adolescence. It is therefore feasible that the salience of the reinforcer in this study, points, contributed to the observed age-related differences in LPP potentiation, whereby the salience of the reinforcer decreased during the course of adolescence. Thus, the reinforcer used in the current study may have had different motivational effects on preadolescents, adolescents and late adolescents, which may have, in turn, influenced the strength of instrumental conditioning, and consequently the magnitude of LPP amplitudes in response to the S^D.

Developmental differences in task performance may have also contributed to the age-related changes in LPP reinforcement-dependent potentiation; preadolescents made significantly more errors during the avoidance block and showed significantly greater LPP potentiation to S^D than both adolescents and late adolescents. Moreover, the main effects of *Condition and Action* in the reward and avoidance blocks, and the *Condition by Age Group* interaction in the reward block failed to reach significance after task accuracy scores were included as a covariate. Critically however, the *Condition by Age Group* and *Action by Age Group* interactions in the avoidance block remained significant when task accuracy was controlled for. However, while preadolescents made the most errors in response to Control^{Go} stimuli in the avoidance block, their LPP amplitudes were greatest for the Avoidance^{Go} S^D. This suggests that the magnitude of the LPP observed does not solely reflect task performance. Hence, while age-related differences in task performance may have partially contributed to age-related differences in LPP amplitude, the findings also suggest that LPP reinforcement-dependent potentiation was modulated by the rewarding and threatening outcomes and the specific response contingencies associated with the S^D.

It is important to note that in contrast to the study predictions and neurobiological models of adolescence (Casey et al., 2008; Ernst et al., 2011; Steinberg, 2008), reward- and threat-related LPP activity was not greater in adolescents (13–17 years old) as compared to preadolescents (9–12 years old) and late adolescents (18–23 years old). Previous fMRI studies that have reported a peak in reward- and threat-related anticipatory activity in adolescents have either used primary reinforcers such as appetitive and aversive tastes (Galván and McGlennen, 2013) or secondary reinforcers such as money (Braams et al., 2015). In this task, points, rather than money, were used as the secondary reinforcer since money may have a different meaning for younger adolescents compared to older adolescents (Barkley-Levenson and Galván, 2014). Thus, the discrepancy between this and previous studies could result from the current study using points as the reinforcer. It is possible that more ecologically valid secondary reinforcers, such as money, or primary reinforcers that have high evolutionary significance are needed to elicit the peak in reward- and threat-related neural activity during adolescence. Significantly however, we found no evidence of a hyporesponsive avoidance system across the adolescent period; in this study reinforcement-dependent potentiation was observed for threat-related cues in the avoidance condition in all three age groups, compared to the reward-related cues where reinforcement-dependent potentiation was found only in preadolescents. Thus, these findings do not support the idea that adolescent behaviour is driven by a hyperresponsive approach system and a hyporesponsive avoidance system (Ernst et al., 2006; Ernst et al., 2011).

Interestingly, in the current study, cues requiring a motor response evoked larger LPP amplitudes in all groups compared to cues requiring inhibition of a motor response. Since the LPP is thought to reflect selective attention to motivationally salient stimuli (Cuthbert et al., 2000; Schupp et al., 2000; Schupp et al., 2004), it is possible that conditions requiring a motor response elicited greater attentional resources in preparation for a motor action. To examine this idea and the possible functional significance of the reinforcement-dependent potentiation of the LPP, the relationships between LPP amplitudes and reaction times were explored. The correlations revealed that LPP amplitudes were not consistently modulated by reaction times. It is possible that the design of our task precluded us from seeing an effect, as there was delay between when the visual cues were presented and when participants were required to make a motor response. Studies have suggested that the LPP reflects a global inhibition of activity in visual cortex, resulting in the selective activity associated with processing the salient stimulus (Brown et al., 2012), and therefore in a local attentional bias (Gable and Harmon-Jones, 2010). Hence, in this study, the stimuli requiring a motor response could be evoking a greater attentional bias compared to stimuli requiring inhibition of a motor response. How and whether this attentional bias can affect subsequent decision making mechanisms and action selection is yet to be determined.

Consistent with previous developmental studies (e.g., Kujawa et al., 2012; MacNamara et al., 2016), overall LPP amplitudes were found to decrease from preadolescence to late adolescence for S^D and control stimuli. The scalp maps also revealed that the LPP topography changed with age, whereby LPP activation shifted from occipitoparietal to centroparietal regions from preadolescence to late adolescence. In addition, the scalp maps revealed that LPP activity became less bilateral and more focal with age. These developmental changes in LPP amplitude and topography are in accordance with previous findings (Dennis and Hajcak, 2009; Hajcak and Dennis, 2009; Kujawa et al., 2012, 2013a, 2013b; Solomon et al., 2012), and are thought to reflect brain maturation during adolescence.

The human brain matures in a back-to-front fashion, with higher order prefrontal regions developing last (Gogtay et al., 2004; Tiemeier et al., 2010). As such, compared to other cortical and subcortical regions, the prefrontal cortex undergoes significant changes throughout childhood and adolescence. Evidence from humans and non-human primates show that there is an overproduction of dendritic spines in the prefrontal cortex during childhood, which is followed by a period of synaptic elimination during early adolescence (Huttenlocher and Dabholkar, 1997; Rakic et al., 1986). Furthermore, the developmental remodelling of the prefrontal cortex continues beyond adolescence and stabilises at adult levels in the third decade of life (Giedd et al., 1999; Petanjek et al., 2011). In addition to these changes in grey matter, there is a linear increase in white matter during childhood and adolescence (Giedd et al., 1999). The maturation of the prefrontal cortex is thought to underlie the considerable improvements in cognitive control and information processing during adolescence (Luna et al., 2004; Yurgelun-Todd, 2007). This is consistent with our behavioural findings showing that preadolescents made significantly more errors on the task compared to adolescents and late adolescents. Moreover, given that both 'top down' prefrontal areas and 'bottom-up' occipitoparietal areas modulate the LPP (Moratti et al., 2011), it is possible that the changes in LPP topography observed in this and other studies (Hajcak and Dennis, 2009; Kujawa et al., 2012; Kujawa et al., 2013b) are the result of the LPP becoming more reliant on prefrontal regions as the prefrontal cortex matures during adolescence.

4.2. N170

While the LPP was used to examine late anticipatory representations to S^D that predicted rewarding and threatening outcomes, the N170 was used to examine early anticipatory representations. The visual stimuli used in our instrumental conditioning task were greeble-like and elicited strong N170 ERPs. This is consistent with previous studies showing that greebles can evoke the N170 component in occipitotemporal regions (Carmel and Bentin, 2002; Gauthier et al., 1999; Levita et al., 2015; Rossion et al., 2002). In contrast to our predictions, N170 amplitudes were not potentiated for S^D compared to control stimuli for any age group. This finding initially appears inconsistent with other studies showing early modulation within ventral visual pathways to motivationally salient stimuli (Dolan et al., 2006; Levita et al., 2015; Pizzagalli et al., 2003), and that biologically and socially salient information modulates activity in the visual cortices in the early stages of information processing (Pizzagalli et al., 2003). In light of this, it is possible that reinforcement-dependent potentiation of the N170 was not observed in this study because we used a secondary reinforcer rather than a primary reinforcer. Previous classical and instrumental conditioning tasks that have shown modulation of the N170 to conditioned stimuli have used a primary reinforcer (a loud aversive tone) where the threat was immediate (Dolan et al., 2006; Levita et al., 2015; Pizzagalli et al., 2003). In the instrumental task used in the present study, we examined reinforcement-dependent potentiation of the N170 to visual cues that predicted the delayed onset of a secondary reinforcer (points) that was dependent on specific response-contingencies. As such, the type of reinforcer used, as well as the delay between the stimulus and response, may have resulted in the discrepancies observed between this and previous studies (Dolan et al., 2006; Levita et al., 2015; Pizzagalli et al., 2003). Future work is needed to identify the task contingencies and reinforcers that elicit reinforcement-dependent potentiation in early visual processing, as well as to identify the functional significance of such potentiation, during adolescence.

Despite not finding reinforcement-dependent potentiation of the N170, we found age-related changes in N170 amplitudes that were independent of condition. In line with previous studies (Hileman et al., 2011; Taylor et al., 1999) and the study predictions, the N170 decreased in amplitude from preadolescence to adolescence. While the scalp topographical plots indicate an additional reduction in N170 amplitudes from adolescence to late adolescence, this effect was not statistically significant.

4.3. Relationships between LPP amplitude and measures of sensation seeking and risk-taking behaviours

An exploratory aim of this study was to examine whether value-related encoding in perceptual areas is associated with increases in risk-taking behaviours and sensation seeking during adolescence. To that end, LPP amplitudes were correlated with sensation seeking and risk-taking behaviours. Correlational analyses were limited to LPP amplitudes since no reinforcement-potentiation was found for the N170. We found that LPP amplitudes correlated with sensation seeking scores in males but not in females, and that the direction of the relationship changed with age. Specifically, preadolescent males had positive relationships between sensation seeking and LPP amplitudes, revealing that greater levels of sensation seeking were associated with greater LPP amplitudes. Interestingly, this relationship disappeared in adolescent males, and reemerged as a negative relationship during late adolescence, showing that greater levels of sensation seeking were associated with smaller LPP amplitudes.

Previous studies have shown that sensation seeking increases during the transition to adolescence and decreases during the tran-

sition to early adulthood (Steinberg, 2004; Steinberg et al., 2008; Stephenson et al., 2003). Moreover, individuals with high sensation seeking levels have an increased desire to seek out novel experiences, and will engage in risky behaviours in order to experience such experiences (Roberti, 2004; Steinberg, 2008). The relationships between sensation seeking and LPP amplitudes observed in this study can be tentatively interpreted in light of these findings. If late adolescent males have reduced perceptual/attentional activation to salient sensory cues in their environment compared to adolescents, as measured by the LPP, they may engage in more sensation seeking behaviours to compensate. By comparison, preadolescent males may be experiencing the natural increases in arousal and sensation seeking associated with the transition from childhood to adolescence (Steinberg, 2010). Finally, it is possible that relationships between sensation seeking and LPP amplitudes were not found for adolescent males since sensation seeking levels peak in middle adolescence, and therefore increases in sensation seeking during early adolescence may have been cancelled out by decreases in sensation seeking in the slightly older adolescent males. However, why this effect was restricted to the males in our sample is unclear and requires further work.

In contrast to sensation seeking, risk-taking behaviours, as measured by the YRBSS, were not associated with changes in LPP amplitudes in any age group. Given that sensation seeking was strongly associated with LPP amplitudes for males, and sensation seeking and risk-taking behaviours are strongly associated (Greene et al., 2000; Hansen and Breivik, 2001), it was surprising that relationships between LPP amplitudes and risk-taking were not found. However, the YRBSS may not have been an optimal measure of risk-taking for this study; the YRBSS measures engagement with risk-taking behaviours on a binary scale and therefore may not reflect the complexity of factors underlying risk-taking behaviours during adolescence (Steinberg, 2007). Consequently, using a more comprehensive measure that assesses the frequency and context of risk-taking may provide more useful insights into the relationships between perceptual processes, action selection, and risk-taking behaviours during the different stages of adolescence.

4.4. Study limitations

The results from the current study need to be considered in light of the study limitations. Firstly, participants in the current study were pooled into three age groups on the basis of similar studies (e.g., Chein et al., 2011; Hare et al., 2008; Padmanabhan et al., 2011; Romer et al., 2009; Van Leijenhorst et al., 2010) and were selected to represent the different stages of adolescence. Categorising participants into three age groups in this study provided a way to assess the anticipatory responses to rewards and threats that were unique to each stage of adolescence. However, grouping participants into categorical age groups instead of using age as a continuous variable can be problematic in developmental research since there are considerable individual differences in the developmental trajectories of children and adolescents (Steinberg and Morris, 2001).

Secondly, while the sample size of the current study is comparable to other studies investigating the development of the N170 and LPP (e.g., Pincham et al., 2015), the sample size of each group is relatively modest and the results should be interpreted with this in mind. Notably, the LPP waveforms and bar graphs (Fig. 3) indicated that there were gender differences in LPP potentiation. Despite this, no gender differences emerged from the statistical analyses. Moreover, Fig. 4 indicated that there were different developmental trajectories for S^D that required a motor response compared to S^D that required inhibition of a motor response that were contingent on the valence of the outcome, but again this effect did not reach statistical significance. Together, these observations suggest that there were high levels of variability in the data and not

enough power to detect potentially interesting effects. Future work should therefore aim to explore the development of reward- and threat-related potentiation in larger samples of adolescents.

Thirdly, the YRBSS is a retrospective self-report questionnaire that measures a range of recent risk-taking behaviours. Critically, there are a number of confounds associated with measuring risk-taking behaviours using self-report questionnaires in developmental samples. For instance, it is possible that developmental differences in risk-taking behaviours will emerge due to older adolescents having greater accessibility to risks (Lejuez et al., 2003). Thus, future work should aim to measure risk-taking in developmental samples using behavioural tasks that assess risk-taking propensity rather than real world risk-taking behaviours.

4.5. Conclusion

Optimal decision-making requires individuals to make actions that maximise reward and minimise loss. Research has repeatedly shown that adolescents are highly motivated by rewards (Ernst et al., 2011; Steinberg, 2008; Van Leijenhorst et al., 2010). However, research examining the extent to which adolescents are motivated by avoiding potential threat is limited. The findings reported here provide initial evidence for developmental differences in value-related encoding in perceptual areas, and suggest that these perceptual biases may be stronger for avoidance-related cues than they are for reward-related cues during adolescence. While future work is required to examine the functional significance of these findings, the results from this study suggest that research should not only focus on sensitivity to reward during adolescence, but also on sensitivity to threat, as both are essential for appropriate social-affective behaviour and development.

Conflicts of interest

No conflicts of interest are declared.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.dcn.2017.03.001>.

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