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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 (Hegdé 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

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