



Developmental changes in the reward positivity: An electrophysiological trajectory of reward processing



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ABSTRACT

Children and adolescents learn to regulate their behavior by utilizing feedback from the environment but exactly how this ability develops remains unclear. To investigate this question, we recorded the event-related brain potential (ERP) from children (8–13 years), adolescents (14–17 years) and young adults (18–23 years) while they navigated a “virtual maze” in pursuit of monetary rewards. The amplitude of the reward positivity, an ERP component elicited by feedback stimuli, was evaluated for each age group. A current theory suggests the reward positivity is produced by the impact of reinforcement learning signals carried by the midbrain dopamine system on anterior cingulate cortex, which utilizes the signals to learn and execute extended behaviors. We found that the three groups produced a reward positivity of comparable size despite relatively longer ERP component latencies for the children, suggesting that the reward processing system reaches maturity early in development. We propose that early development of the midbrain dopamine system facilitates the development of extended goal-directed behaviors in anterior cingulate cortex.

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1. Introduction

Impulsive behaviors are a hallmark of childhood and adolescence but typically subside in adulthood. This transition is thought to arise from the asynchronous development of two neural systems, first by a “bottom-up” system motivated by immediate rewards, followed by a “top-down” system for cognitive control that regulates impulsive behavior (Casey et al., 2005, 2008; Spear, 2013; Geier, 2013). Brain regions supporting inhibitory control such as prefrontal cortex (PFC) and dorsal anterior

cingulate cortex (ACC) exhibit protracted development (Fuster, 2002; Geier, 2013) and increasing task-relevant activation (Ordaz et al., 2013) throughout this period. Consistent with dual-systems models of control (Hofmann et al., 2009), PFC is believed to facilitate execution of task-appropriate behavior by applying control signals that bias information processing in the basal ganglia (BG) and other brain areas (Miller and Cohen, 2001). By contrast, ACC is central to several theories of cognitive control but its specific function remains controversial (Mars et al., 2011).

We have recently proposed that ACC motivates the selection and execution of extended goal-directed behaviors according to principles of hierarchical reinforcement learning (Holroyd and Yeung, 2012). On this account, ACC temporally integrates the value of reward signals carried by the midbrain dopamine (DA) system to learn which tasks are most worth performing, and then selects particular tasks for execution based on the learned values. Once a task

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is selected, ACC directs PFC to apply top-down control over task execution by the BG and other brain areas (Holroyd and Yeung, 2012; Holroyd, 2013; see also Holroyd and McClure, submitted for publication; Umemoto and Holroyd, submitted for publication). This theory develops a previous proposal that ACC uses reward prediction error (RPE) signals carried by the midbrain DA system to learn the value of action policies (Holroyd and Coles, 2002; Holroyd and Yeung, 2012). It has been suggested that phasic increases in DA activity encode positive RPE signals that indicate when ongoing events are better than expected, and phasic decreases in DA activity encode negative RPE signals that indicate when ongoing events are worse than expected (Schultz et al., 1997), which shape behavior adaptively according to principles of reinforcement learning (Sutton and Barto, 1998). We might therefore expect both ACC and DA to play key roles in the development of behavioral regulation.

The ability to learn from reinforcement continues to develop into adolescence in parallel with the development of self-regulatory control (Crone et al., 2004; Huizinga et al., 2006; van den Bos et al., 2012). During this period connections between PFC and striatum are refined through pruning and enhanced axonal connectivity (Rubia, 2012). Further, the relatively prolonged development of ACC (Crone et al., 2008; Fjell et al., 2012) appears to be responsible for age-related improvements in self-regulation (Velanova et al., 2008). Although the development of the DA system is complex and poorly understood, changes in the relative density of DA receptors in cortical and subcortical structures have been observed (Wahlstrom et al., 2010). Additionally, it has been proposed that increases in tonic DA levels during adolescence encourage exploratory behaviors, allowing for greater exposure to rewarding stimuli (Luciana et al., 2012). Research with rodents has also indicated that tonic dopamine levels code for average reward rate that may be important for motivating behavior (Niv, 2007) and for promoting cognitive flexibility (Floresco, 2013). As learning from explicit rewards has been shown to be dependent on phasic DA responses (Schultz, 2013), it is possible that the simultaneous maturation of the ACC and DA systems may facilitate the development of a cognitive mechanism for reinforcement learning and control.

This developmental trajectory may be evident in a component of the event-related brain potential (ERP) called the reward positivity, which we have proposed reflects the impact of DA RPE signals on ACC for the purpose of adaptive decision making (Holroyd and Coles, 2002; Walsh and Anderson, 2012). Also known as the feedback error-related negativity or feedback-related negativity, the reward positivity appears around 250 ms following the presentation of feedback stimuli, is characterized by a frontal–central scalp distribution, and is sensitive to the valence of feedback stimuli (Miltner et al., 1997). Recent developments of this idea hold that the difference between ERPs elicited by positive and negative feedback results from dopaminergic modulation of the amplitude of the N200, a negative-going ERP component produced in ACC that is generated by unexpected task-relevant events. According to this position, unexpected rewards produce a phasic increase in DA that suppresses the N200, resulting in the reward positivity

(Holroyd et al., 2008b; see also Baker and Holroyd, 2011; Hajihosseini and Holroyd, 2013).

The reward positivity provides a means for assessing the developmental trajectory of behavioral regulation but to date only a few studies have examined this ERP component in typically-developing children and adolescents. In pre-school aged children, Mai and colleagues (2011) found no difference in the amplitudes of the ERPs elicited by positive and negative feedback. Eppinger et al. (2009) reported that, relative to young adults, 10–12 year old children produced larger N200 amplitudes to negative feedback, whereas Hämmerer et al. (2011) observed that 9–11 year old children produced larger N200 amplitudes to both positive and negative feedback. Of four studies that examined the reward positivity in adolescents and young adults, three reported no difference between adolescents (13–14, 16–17 and 15–17, respectively) and young adults (Hämmerer et al., 2011; Santesso et al., 2011; Yi et al., 2012) and the fourth study found that male adolescents (14–17) produced a relatively smaller reward positivity (Zottoli and Grose-Fifer, 2012).

These mixed results could stem in part from varying approaches to measuring the reward positivity (see Section 4 below), or to the use of tasks with relatively complex schedules for reward probability and magnitude that could exacerbate the potential for component overlap with other, non-reward related ERP components (San Martin, 2012). Given that the reward positivity is said to index neural systems critical to the development of self-regulation, that it is used increasingly to study atypical development (e.g., Holroyd et al., 2008a), and that ERP morphology differs widely between children and adults (Johnstone et al., 2005; Coch and Gullick, 2012), it is important to establish how the reward positivity develops in a typical population. For these reasons we recorded the ERP from children, adolescents and young adults as they searched for rewards in a relatively engaging “virtual maze” task that produces a canonical reward positivity (Baker and Holroyd, 2009). We predicted that reward positivity amplitude would increase with age, reflecting the developing maturity of the cognitive control system.

2. Method

2.1. Participants

For the purposes of statistical comparison, 60 participants were categorized into three groups based on age: 20 children ages 8–13 (10.0 ± 1.7 years, 11 males), 20 adolescents ages 14–17 (15.6 ± 1.0 years, 10 males), and 20 adults ages 18–23 (19.7 ± 1.4 years, 7 males). Two additional participants were excluded due to incomplete data. Children and adolescents were recruited through a local newspaper ad, fliers posted throughout the community and Facebook event advertisements. The adult sample was obtained through the University of Victoria psychology participant pool. All participants received a performance-related bonus of CDN \$5 at the end of the task (see below). In addition, at the conclusion of the experiment, university students received course credit, adolescents received CDN \$14 (\$7.00/h), and children and their parents received small

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