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Developmental continuity in reward-related enhancement of cognitive control

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ABSTRACT

Adolescents engage in more risky behavior than children or adults. The most prominent hypothesis for this phenomenon is that brain systems governing reward sensitivity and brain systems governing self-regulation mature at different rates. Those systems governing reward sensitivity mature in advance of those governing self-control. This hypothesis has substantial empirical support, however, the evidence supporting this theory has been exclusively derived from contexts where self-control systems are required to regulate reward sensitivity in order to promote adaptive behavior. In adults, reward promotes a shift to a proactive control strategy and better cognitive control performance. It is unclear whether children and adolescents will respond to reward in the same way. Using fMRI methodology, we explored whether children and adolescents would demonstrate a shift to proactive control in the context of reward. We tested 22 children, 20 adolescents, and 23 adults. In contrast to our hypothesis, children, adolescents, and adults all demonstrated a shift to proactive cognitive control in the context of reward. In light of the results, current neurobiological theories of adolescent behavior need to be refined to reflect that in certain contexts there is continuity in the manner reward and cognitive control systems interact across development.

1. Introduction

Adolescents engage in more risky behaviors than children or adults (Steinberg, 2010). For example, seventy-two percent of adolescent mortality is the result of preventable causes, such as accidents, suicide, and homicide (Eaton et al., 2008). Because these risk-taking behaviors are a public health concern, identification of the neurodevelopmental changes underlying them may lead to new insights for effective preventative interventions.

One hypothesis about why adolescents engage in risky behavior is that youth experience a mismatch in the maturation rate of relevant brain systems. Consistent with this view, there is evidence that brain systems involved in reward sensitivity – which might draw adolescence towards certain features in the environment – mature in advance of brain systems involved in cognitive control – which might help adolescents regulate their behavior. This maturational asynchrony may contribute to risk-taking because adolescents may be overly compelled by some features of the environment without the appropriate checks-and-balances afforded by control or regulatory circuitry (Somerville et al., 2010; Steinberg, 2010). However, we know relatively little about the ways that these reward and control systems might interact. This is because most of the existing research in this area has been focused upon situations in which cognitive control systems must regulate or constrain reward sensitivity systems. In contrast, less

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is understood about situations where reward sensitivity promotes cognitive control.

The present experiment was designed to begin to address this issue.

One test of how the cognitive control system regulates the reward system is the Iowa Gambling Task (Bechara et al., 1994). In this paradigm, participants must learn to avoid a deck of cards with high potential reward because it is also associated with high potential loss. To do this, the participant must exert cognitive control to suppress the impulse, driven by reward motivation, to choose the high-risk deck. Avoiding these high-risk situations allows participants to ultimately earn the most money over the course of the experiment, which in the context of this paradigm is adaptive behavioral performance. Unlike adults, in this context, adolescents typically choose the high reward/high risk deck more frequently than adults (Cauffman et al., 2010). Developmental changes in performance on the Iowa Gambling Task have also recently been examined using fMRI, and it has been found the prefrontal cortex (PFC), a central node of the cognitive control network, is increasingly engaged with age (Christakou et al., 2013). These findings suggest that inhibition of reward sensitivity through cognitive control is a mechanism underlying adaptive behavior. Yet there are also situations where adaptive behavior requires the opposite pattern, where it is reward systems that serve to promote cognitive control. As a case in point, individuals often perform better across a variety of challenging tasks when offered rewards (Geier et al., 2010; Jimura et al., 2010; Locke and Braver, 2008). Indeed, there is evidence that reward leads to improvements in cognitive control performance through a shift in cognitive control strategy (Braver, 2012). In sum, there appear to be many ways in which reward and cognitive control systems become integrated over development. Understanding imbalances in the interaction of these systems may shed light on some of the maladaptive behaviors, such as risk-taking, often observed in adolescents.

1.1. Reward, cognitive control, and development

A great deal has been learned about the neural mechanisms that support cognitive control in adults. Cognitive control is facilitated by a distributed network of brain regions, localized mainly in lateral prefrontal, parietal, and anterior cingulate cortices (Owen et al., 2005; Wager and Smith, 2003). Current theories suggest that cognitive flexibility is enabled by dual-modes of cognitive control (Braver and Barch, 2002). Adults are able to activate either proactive or reactive modes of cognitive control. In the proactive mode, information that is important to an individual's objective is maintained in the time period before self-control is required. For example, awareness that one needs to drive home at the end of the evening would lead an individual to anticipate being offered the next alcoholic drink and prepare a response to decline it. Reactive cognitive control reflects operations invoked subsequent to a stimulus. In keeping with the example above, after being offered another alcoholic drink, an individual would consider his/her situation and responsibility and then decline the offer. In the laboratory setting the AX-Continuous Performance Task (AX-CPT) has frequently been used to study proactive and reactive control. In this task participants are presented with a letter that serves as the cue (A or B) followed by a letter that serves as the probe (X or Y). Participants are instructed to press a button under his/her index finger when the letter "A" is followed by the letter "X", and to press the button under his/her index finger for all letter combinations. When participants engage in proactive strategy they primarily attend to the cue and in contrast if they employ a reactive strategy they primarily attend to the probe (Braver et al., 2009). Using this task, it has been demonstrated that reward motivation such as financial reward for good performance, leads adults to engage a proactive strategy of cognitive control which is also associated with better behavioral performance (Jimura et al., 2010; Locke and Braver, 2008).

One way that researchers have measured whether individuals implement proactive or reactive cognitive control strategies is through mixed block/event-related designs in functional magnetic resonance imaging (fMRI) (Visscher et al., 2003). With this type of design, the participant is presented with a series of trials separated by large periods of rest. This allows investigators to determine whether brain regions remain active across the group of trials (sustained activation) or whether the brain regions are engaged and disengaged with the presentation and termination of each individual trial (transient activation). Sustained brain activation is hypothesized to index proactive cognitive control as the brain regions are engaged across a block of trials independent of the stimulus presentation (Jimura et al., 2010). Additionally, sustained activation of the fronto-parietal network is associated with behavioral indices of proactive cognitive control (Locke and Braver, 2008; Jimura et al., 2010), and the fronto-parietal network has been consistently implicated in cognitive control (Owen, 2005; Dosenbach et al., 2008).

There are age-related changes in cognitive control and reward sensitivity across adolescence (Luna et al., 2010), though findings about the neural correlates of these changes are unclear. In terms of the cognitive control system, and whether there is greater or lesser activity in these regions across development, it appears to depend in part on the task and analysis. It has been demonstrated on a task of inhibitory control that trial-related activity decreases with age, while sustained activity increases with age (Velanova et al., 2009). Still other studies suggest different brain regions are engaged across development (Bunge et al., 2002). Despite the inconsistency in directionality, it does appear that cognitive control circuitry is engaged differentially across development, and that maturation of this circuitry is related to behavioral differences (Crone and Dahl, 2012).

A number of studies have found adolescents, relative to adults, show heightened neural responses to reward (Christakou et al., 2011; Ernst et al., 2005; Galvan et al., 2006; Geier et al., 2010; Padmanabhan et al., 2011; Smith et al., 2011). Some studies have found an underactivation of reward circuitry in adolescents relative to adults (Bjork et al., 2004; Bjork et al., 2011), however they seem to be the exception. Generally, it is accepted that adolescents exhibit

a heighted sensitivity to reward (Crone and Dahl, 2012). This combination of rapidly maturing reward sensitivity and immature cognitive control abilities is hypothesized to promote the peak in risk-taking observed during adolescence (Steinberg, 2010). The majority of related research to date has focused on contexts where heightened reward sensitivity and immature cognitive control would be likely to promote maladaptive behavior. These contexts include a series of gambling and decision-making tasks (Chein et al., 2011). In these contexts, cognitive control must be used to regulate reward sensitivity in order to promote adaptive behavior.

In contrast, a handful of studies have begun to address the question as to whether the manner that reward influences cognitive control changes across development (Geier et al., 2010; Padmanabhan et al., 2011). These investigations examined both behavior and event-related brain activity. In contrast to the investigations on reward and decision-making (Chein et al., 2011; van Leijenhorst et al., 2010), Geier et al. (2010) and Padmanabhan et al. (2011) found that across development, reward improves cognitive control. In these investigations participants preformed a cognitive control task with and without a monetary reward for good performance. Children and adolescents were more accurate on trials where they were rewarded, and all three age groups (children, adolescents, adults) responded more quickly on reward trials (Geier et al., 2010; Padmanabhan et al., 2011). Although, all age groups showed similar behavioral improvements in cognitive control, in the context of reward, these studies also identified differences in neural engagement. These are very important studies as they provide evidence that reward can lead to improvements in cognitive control, even while the brain is still developing. These studies also suggest that the neural mechanisms responsible for the behavioral improvement associated with reward may change across development. A limitation of this body of work is that only transient (or event-related) brain activity was measured and consequently we are unable to determine whether children and adolescents, like adults, increase proactive control in the context of reward.

1.2. Present investigation

The present study was designed to investigate whether reward promotes improvements in cognitive control for children and adolescents. We also examined whether reward led children and adolescents to shift their cognitive control strategies in a manner similar to adults. If children and adolescents respond to reward in the same way as adults, it would suggest that some aspects of the integration between reward sensitivity and cognitive control systems is present as early as childhood. Further, it would suggest that the maladaptive behavior that is often observed in adolescents could not simply be attributed to a general lack of integration between reward and cognitive control systems.

To address these questions, we used a mixed block/event-related fMRI design to examine whether children and adolescents demonstrate an increase in proactive cognitive control in the context of reward. We indexed proactive cognitive control through the magnitude of sustained activation during task blocks, and we expected greater sustained activation in reward blocks as compared to neutral blocks. Three samples of participants – children, adolescents and adults – completed an AX-CPT cognitive control task under neutral and reward conditions. The experimental paradigm was designed to allow us to estimate sustained brain activity (our index of proactive cognitive control) while controlling for event-related (transient) fluctuations. We hypothesized that, as compared to adults, adolescents would demonstrate less of an increase in proactive cognitive control in the context of reward. We tested this hypothesis by evaluating the magnitude of change in sustained brain activity from neutral to reward blocks. This approach is consistent with previous investigations which have found that the magnitude of sustained brain activity reflects an index of proactive cognitive control in adults (Andrews-Hanna et al., 2011; Velanova et al., 2009). We also tested a group of young children to help clarify whether differences between adolescents and adults reflects (a) immature cognitive control circuitry in adolescents or (b) an imbalance in maturity between reward and cognitive control abilities. If children and adolescents perform similarly, this would be consistent with the view that reward and cognitive control systems become increasingly integrated over the course of development. However, if younger children and adults demonstrate an increase in proactive cognitive control, not observed in adolescents, this would suggest that the ability to shift cognitive control strategies within the context of reward is impaired during adolescence.

2. Materials and method

2.1. Participants

Participants in this investigation were 23 adults (M = 27 years, 2 months, SD = 18 months, range = 25–30 years) 20 adolescents (M = 15 years, 1 month, SD = 8 months, range 14–16 years) and 22 children (M = 10 years, 5 months, SD = 9 months, range 9–11 years). An additional 6 adolescents and 6 children participated in the investigation. The adolescents were excluded because of a problem with the stimulus presentation software, and the children were excluded because of excessive motion. All participants gave informed consent (parental consent and minor assent for adolescents and children) for a protocol approved by the Health Sciences Institutional Review Board of University of Wisconsin-Madison. Compensation was provided for participation, in terms of base amounts for the fMRI session $80, plus an additional bonus of $30 from the monetary incentives provided at the end of the session. All participants received the same amount of incentive bonus ($30).

2.2. Experimental task

The impact of reward on cognitive control was assessed at both the behavioral and neural level. Participants were asked to complete a variant of the continuous performance

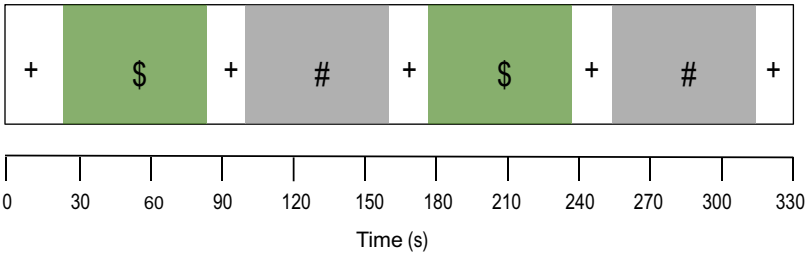

Fig. 1. Schematic depiction of an fMRI run. Each run contained two blocks of reward trials and 2 blocks of neutral trials. The order of blocks was different in each run. All blocks contained 10 trials and lasted 60 s. Blocks were separated periods of fixation that lasted 16 s. Additionally the task began with a period of fixation that lasted 24 s.

test (CPT), the AX-CPT (Rosvold et al., 1956) while undergoing fMRI under blocked reward-incentive and no-incentive (neutral) conditions.

Participants completed 3 runs of the task, which each lasted 5 min and 30 s. Within each run there were 4 blocks of trials, which lasted 1 min, and were separated from adjacent blocks by a period of fixation. Each block was exclusively comprised of reward or neutral trials (Fig. 1).

There were 10 trials within each block. The sequence of events for reward and neutral trials is presented in Fig. 2. During reward trials participants saw a dollar sign followed by the contextual cue (the letter "A" or "B") a delay period, and then the probe (the letter "X" or "Y"). Participants were instructed to press the button under their index finger when they saw an "A" followed by an "X", and to press the button under their middle finger for all other letter combinations. When participants responded correctly and prior to the time limit, the trial was successful and participants saw a green dollar sign. For neutral trials the events were identical, except participants saw a pound sign at the beginning of each trial and saw the word "correct" if the trial was successful. For both conditions participants received no feedback if they responded incorrectly or subsequent to the time limit.

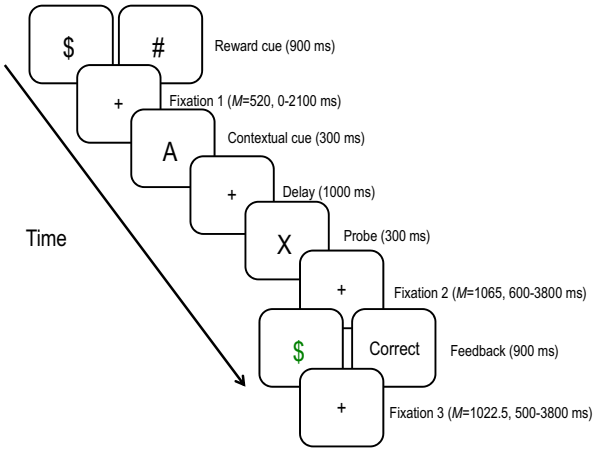

Fig. 2. Depiction of events in the AX-CPT task. Within reward blocks, each trial was preceded by a dollar sign. In neutral blocks each trial was preceded by the pound sign. All trials consisted of a contextual cue, a probe, and feedback on accuracy and performance. Feedback for correct trials was a green dollar sign in reward blocks, and the word "Correct" in neutral blocks.

For all trials, participants were instructed to respond as quickly and accurately as possible. Target trials (AX) were the most prevalent (70%) and all other trial types (AY, BX, BY) had an equally low frequency (10% each). The prespecified reaction time cutoff was used for all trials and was set individually for each participant. This was based on each participant's performance during a 5 min long practice session that was completed prior to the scanning session. The cutoff was the 30th percentile (ordered from fastest to slowest) of correct response times (RTs) in the practice session. The performance criterion was chosen to avoid ceiling effects, and has been used previously in a similar experiment (Jimura et al., 2010). Prior to the scanning session, participants were informed that depending on the number of green dollar signs they received across the entire experiment they could earn up to an additional $30, but it was important that they tried their best on both reward and neutral trials.

In order to permit independent estimation transient activation (trial-related activity), the duration of the periods of fixation were jittered, and the order of trial types varied across blocks. Random durations of fixation, and order of events were created using Make_Random_Timing (http://afni.nimh.nih.gov/pub/dist/doc/program_help/make_random_timing.py.html) and the efficiency of the design was assessed using 3dDeconvolve. One hundred different possible stimulus presentations were generated, and the most efficient design was chosen. Within each block there were 34 s of stimulus presentation, and 26 s of fixation.

Stimuli were presented using E-Prime software (Psychology Software Tools, Pittsburgh, PA) via a fiber optic goggle system (Avotec, Stuart, FL) with a screen resolution of 800 × 600 pixels.

2.3. Image acquisition

Images were collected on a General Electric 3 Tesla scanner (GE Medical Systems, Waukesha, WI) equipped with a standard whole-head transmit-receive 8 channel head coil. Functional images were collected using a T2*-weighted gradient-echo, echo planar imaging (EPI) pulse sequence [42 sagittal slices, 3.5 mm thickness; 64 × 64 matrix; 224 mm (FOV); repetition time (TR)/echo time (TE)/Flip, 2000 ms/25 ms/60°, 165 whole-brain volumes per run]. A high-resolution T1-weighted anatomical image was also acquired (T1-weighted inversion recovery

fast-gradient echo; 256 × 256 in-plane resolution; 256 mm FOV; 256 mm × 1 mm axial slices).

2.4. Image analysis

Individual participant data was slice-time, and motion corrected using AFNI (Cox, 1996). In order to evaluate participants' movement objectively, in-house developed software was used to identify frames where a point chosen relative to the center of rotation was displaced more than 2 mm. A priori, it was decided that any participants who had more than 25% of frames excluded within any run would be excluded from further analyses. Based on this criterion, 6 children were excluded, as noted above. Of the remaining participants, 8 children ($M = 8.5/495$ frames, $SD = 6.7$), and 5 adolescents ($M = 5.8/495$ frames, $SD = 3.4$) had frames censored.

An omnibus GLM was conducted for each participant using regressors to estimate both sustained and event-related effects. Regressors to estimate sustained effects consisted of two boxcar functions convolved with an ideal hemodynamic response (one for Reward blocks, and one for Neutral blocks), which had the duration of the block (60 s). Transient task-related effects were estimated with 5 boxcar regressors convolved with an ideal hemodynamic response. Trials with an "A" cue, and a "B" cue were modeled separately for both the reward and neutral conditions. The events were time-locked to the onset of the contextual cue and had a duration of 1.6 s, which included the delay period and probe. Incorrect trials were modeled separately. In addition to the regressors that were included to model effects of interest, we also included a second order polynomial to model the baseline and slow signal drift. To model possible variance due to motion, we included six predictors (3 translation, 3 rotation) based upon estimated motion (Johnstone et al., 2006).

The parameter estimates, obtained from the GLM, were converted to percent signal change values, normalized to the MNI152 standard brain space using the AFNI program @auto_tlrc, and smoothed using a 6 mm full-width at half-maximum Gaussian filter. It has been demonstrated that despite anatomical differences related to development, normalization done in this way results in brain morphology that does not differ between children and adults (Burgund et al., 2006).

To determine whether the brain regions involved in cognitive control demonstrated an increase in sustained activation in the context of reward and whether this effect differed across age groups,we focused our analyses on the brain regions involved in cognitive control. To do this, we used a mask of brain regions involved in cognitive control derived from meta-analyses (Owen et al., 2005; Wager and Smith, 2003). This mask has been used in previous investigations of reward and cognitive control (Locke and Braver, 2008) and consists of frontal and parietal regions. Mean parameter estimates were extracted using the mask, and additional analyses were conducted using SPSS 19 (SPSS, Chicago, IL) to identify age, condition, and age × condition effects.

3. Results

3.1. Impact of reward on cognitive control

We first tested whether all age groups would demonstrate better behavioral performance in the context of reward. In order to minimize performance differences, which may cause differences in brain activation, task difficulty was titrated to be consistent with a participant's ability. Accuracy was very high for both conditions (Fig. 3), and not affected by the presence of reward, $F(1,62) = .002$, $p = ns$. Although younger participants performed slightly worse than older participants, $F(2,62) = 8.95$, $p < 001$, there was no interaction between reward context and age, $F(2,62) = .088$, $p = ns$. While accuracy did not differ between the conditions, reaction time did. Participants responded more quickly during reward trials ($M = 404.95$, $SE = 12.62$) as compared to neutral trials ($M = 426.13$, $SE = 13.38$) $F(1,62) = 31.91$, $p < 001$. There was no effect of age $F(2,62) = 2.17$, $p = ns$. There was, however, an interaction between age and condition $F(2,62) = 3.74$, $p = 029$. All participants responded more quickly on reward trials. Follow up t-tests revealed that the difference in reaction time between reward and neutral trials was larger for children ($M = 34.88$, $SD = 43.14$) than it was for adults ($M = 10.83$, $SD = 18.95$), $t(43) = 2.44$, $p = .19$. There was no difference between children and adolescents ($M = 17.83$, $SD = 43.14$), $t(41) = 1.12$, $p = .27$, or adolescents and adults $t(40) = 1.58$, $p = .12$.

Adults, adolescents, and children demonstrated a similar improvement in cognitive control in the context of reward. The best measure of cognitive control performance within this task is the percentage of successful trials. In order for a trial to be considered successful, a participant had to both respond quickly (prior to the time limit) and accurately. Participants were successful on a higher percentage of trials in the Reward Condition ($M = 76.8$, $SD = 15.32$) as compared to the Neutral Condition ($M = 72$, $SD = 16.12$). There was no effect of age, $F(1,62) = 1.36$, $p = ns.$, nor an interaction between age and reward context, $F(2,62) = .215$, $p = ns.$, on the percentage of trials that were successful (Fig. 4).

3.2. Proactive cognitive control and reward

Previous research has indicated that adults exhibit better cognitive control performance when they are rewarded for good performance. This research also indicates that improvement in cognitive control is facilitated by a shift to proactive cognitive control (Locke and Braver, 2008). To determine whether children and adolescents demonstrated this increase in proactive control that has been observed in adults, we examined sustained brain activation within the cognitive control network using a Region of Interest (ROI) approach for each of the three age groups. The parameter estimates for the block-related activity were extracted for Reward and Neutral blocks. Repeated-measures ANOVAs were conducted for each cluster with condition (Neutral, Reward) as a within-subjects factor and Age (Children, Adolescents, Adults) as a between-subjects

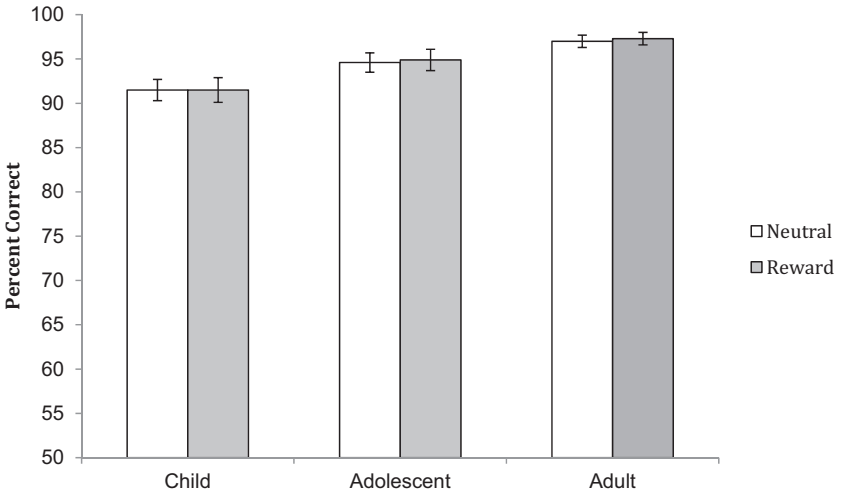

Fig. 3. Accuracy by condition (Neutral, Reward) and age group (Children, Adolescents, Adults). There were no differences between conditions, but children were less accurate than adults. The black vertical bars represent the standard error of the mean.

Table 1
Regions of interest from the from the cognitive control network which demonstrated an effect of Condition (Reward, Neutral), Group (Adult, Adolescent, Child), and/or Group by Condition. All condition effects were driven by an increase in the magnitude of the sustained activation in the Reward Condition relative to the Neutral Condition.

Brain regions	MNI coordinates			Condition		Group		Group × Condition	
	x	*y*	*z*	*p*	η_p^2	*p*	η_p^2	*p*	η_p^2
Cerebellum	28	−58	26	.994		.007	.148	.443	
R. Inferior Parietal	34	−49	39	.000	.211	.679		.398	
L. Inferior Frontal G.	−36	39	13	.006	.115	.739		.954	
R. Inferior Frontal G.	40	32	28	.000	.221	.927		.934	
L. Parietal	−36	−49	40	.012	.098	.955		.784	
R. Precentral G.	28	2	50	.005	.118	.848		.827	
L. Precentral G.	−44	9	29	.008	.107	.520		.368	
L. Precuneus	−12	−66	46	.013	.095	.218		.258	
R. Inferior Frontal G.	44	3	26	.003	.136	.806		.457	
Cerebellum	−26	−66	−39	.029	.074	.037	.101	.602	
R. Anterior Insula	34	31	−5	.001	.162	.259		.896	
R. Cuneus	4	−81	11	.046	.063	.824		.747	
R. Precuneus	12	−60	47	.010	.101	.811		.079	.078
R. Inferior Frontal G.	36	47	14	.003	.132	.253		.801	
R. Thalamus	10	−13	4	.002	.140	.438		.447	

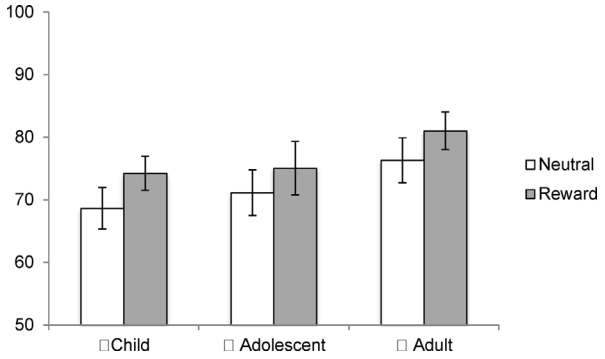

Fig. 4. Percent of successful trials in the Neutral (where participants saw "Correct") and Reward (where participants saw "$") conditions. In order for a trial to be successful a participant needed to respond correctly and prior to the time limit. All participants had more successful trials during the reward condition. The black vertical bars represent the standard error of the mean.

factor. Table 1 provides a summary of all ROIs in which we observed a main effect of reward context in sustained brain activation. During reward blocks, participants exhibited increased activation in frontal and parietal regions relative to neutral blocks (Fig. 5). Consistent with previous reports, the right lateral PFC was a region that was more active in the reward condition (Locke and Braver, 2008). This pattern was consistent across children, adolescents, and adults.

Engagement of these brain regions, and the manner that engagement of these regions was modulated by the reward context, was remarkably similar across age groups. Of the 21 ROIs, effects of age were identified in only two regions of the cerebellum. There was a trend in the right precuneus for an interaction between age and reward, $F(2,62) = 2.64$, $p = .79$. Follow up *t*-tests revealed that this region was more active in the Reward Condition for children, $t(21) = 2.84$, $p = .01$ and adults $t(22) = 2.40$, $p = .02$. Of note, adolescents did not demonstrate any difference in

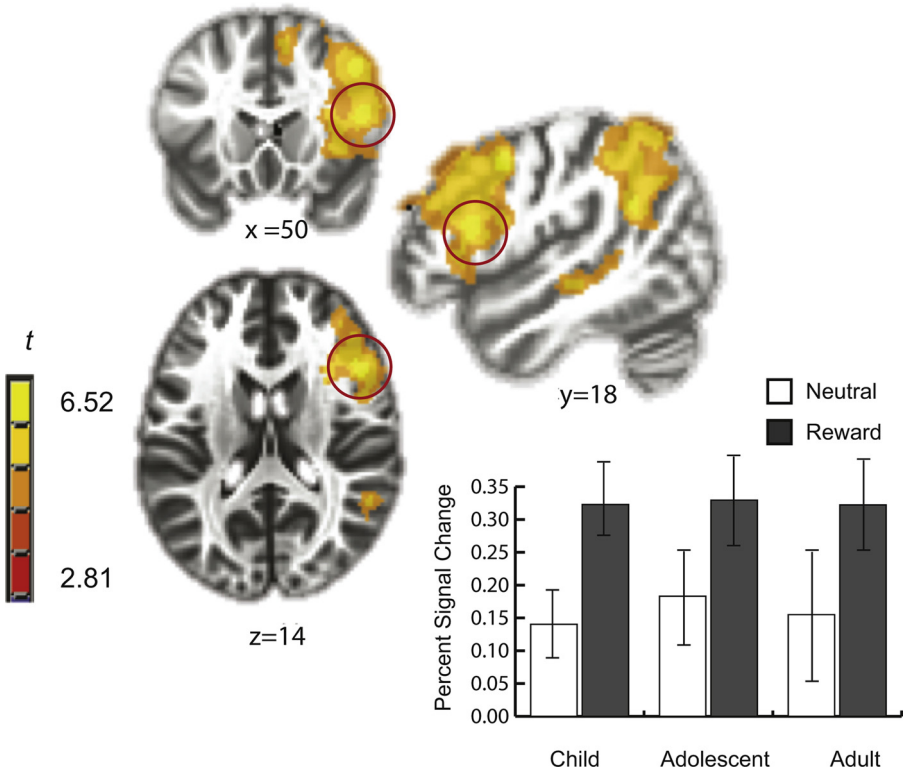

Fig. 5. Brain regions that demonstrated an increase in sustained activity from Neutral to Reward blocks. All voxels are significant at $p < .005$. Within the circled region, the percent signal change was extracted from a sphere, with a radius of 6 mm, centred over the peak of the activation. The bar graphs represent the mean percent signal change, and the black vertical bars represent the standard error of the mean.

activity within this region between the two conditions, $t(20) = .117$, $p > .05$ (Fig. 6).

4. Discussion

The current study was designed to investigate whether children and adolescents demonstrate an increase in proactive control in the context of reward. We tested this hypothesis by evaluating the magnitude of change in sustained brain activity, within the cognitive control network, from blocks of neutral trials to blocks of rewarded trials. To examine possible developmental changes in this process, we contrasted sustained brain activation among children, adolescents, and adults. We found remarkable consistency in the pattern of results across these age groups. Our experimental design titrated the difficulty of the task based on participants' abilities, therefore, the similar patterns of sustained brain activation within the cognitive control network cannot be an artifact of age-related performance issues. There was one area where adolescents differed from both children and adults: children and adults demonstrated an increase in sustained activation within the right precuneus, but adolescents did not.

Taken together, these results demonstrate that, as early as childhood, individuals demonstrate an increase in proactive control in the context of reward. These data do not suggest an imbalance in the maturity of reward and cognitive control systems during adolescence. Indeed, adolescents utilized systems to facilitate proactive cognitive control in a manner very similar to adults.

4.1. Developmental differences in brain activation

We observed only one difference among the adolescents. Unlike children and adults, adolescents may not have had an increase in sustained activation within right precuneus in the context of reward. The meaning, significance, and effect size of this difference requires further investigation. The precuneus is a region that has been implicated in age-related changes in cognitive control (see Crone and Dahl, 2012 for a review). This difference could reflect changes in the integration of reward and cognitive control systems during adolescence. At the same time, it is noteworthy that there is a great deal of continuity in these systems across development.

The pattern of results we observed replicates previous findings in adults (Locke and Braver, 2008), and extends them to both children and adolescents. However, our paradigm differs slightly from that of Locke and Braver (2008). That 2008 experiment was focused on the impact of motivation on cognitive control. For this reason, a different time limit was used for reward and neutral trials. In contrast, we specifically sought to examine the impact

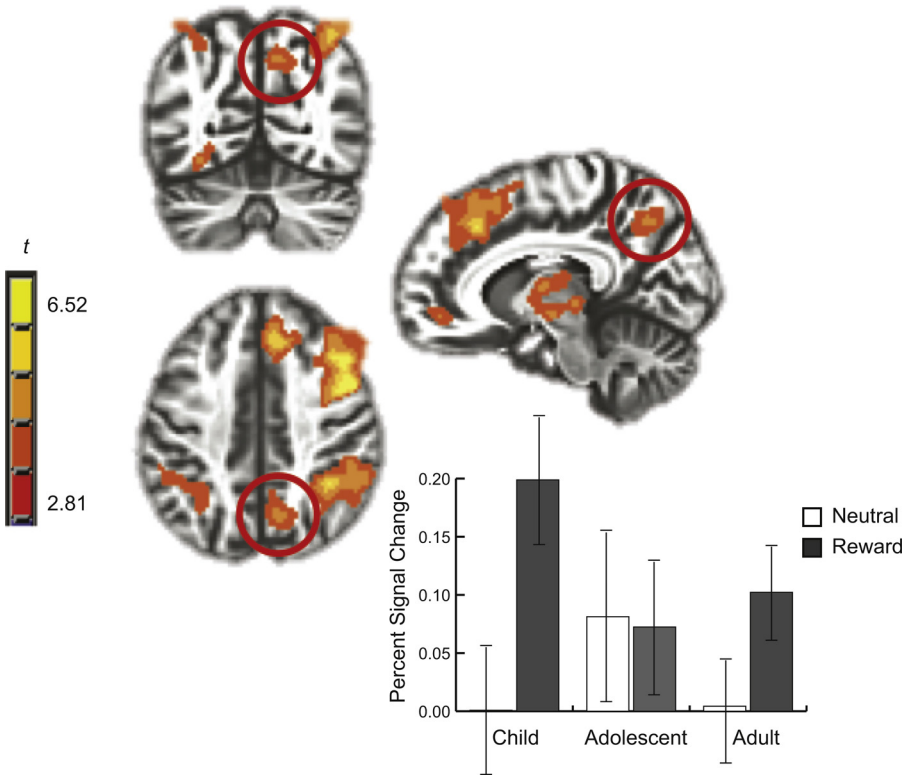

Fig. 6. Regions that demonstrated an increase in sustained activity from Neutral to Reward blocks, and all voxels are significant at $p < .005$. The circle region is the area where there was a trend for an interaction between age and condition. The bar graph is the mean percent signal change extracted from the circled cluster. The black vertical bars represent the standard error of the mean.

of reward on cognitive control, and therefore kept the task demands similar across conditions.

4.2. Reward facilitated cognitive control across development

This investigation adds to an emerging body of literature demonstrating that reward promotes improvements in cognitive control across development (Geier et al., 2010; Padmanabhan et al., 2011; Smith et al., 2011). Across a variety of cognitive control tasks (anti-saccade, sustained attention) participants varying in age from young children to older adults all perform better (fewer errors and more rapid responses) when a monetary reward is provided for good performance. These studies have catalogued a number of differences in the brain regions engaged across development, however the behavioral significance of these differences remains unclear.

Given the widely held view that adolescents have a maturational lag in their cognitive control abilities, it is noteworthy that we did not find age-related differences in the shift to proactive control. Children, adolescents and adults all demonstrated an increase in sustained activity within the majority of the cognitive control network. Even the magnitude of this response was similar across age groups. This is the first reported study, that we are aware of, to demonstrate that the neural mechanisms that support reward-related improvements in cognitive control are in place and functional as early as childhood. These findings should help refine current theories of adolescent risk-taking.

4.3. Limitations and future directions

A potential limitation of this experiment is that the task was relatively easy for all participants. This was an intentional component of the experimental design intended to eliminate confounds of age-related performance differences on brain activation. However, subsequent studies may begin to test the effects of cognitive challenge on these systems across development. It may be only when cognitive resources are challenged, that age-related differences in neural engagement are likely to emerge.

5. Conclusion

In this investigation we found that like adults, children and adolescents exhibit better cognitive control when they are provided with a reward for good performance. Across all age groups the improvement in cognitive control appears to be facilitated by a shift to proactive cognitive control. All participants demonstrated an increase in sustained brain activation within the cognitive control network, including the right lateral PFC. These results were in contrast to our hypothesis. We expected to see a different pattern of brain activation in adolescents, given

the dual-systems perspective (Somerville and Casey, 2010; Steinberg, 2010), which suggests that adolescence is a transition period where the interaction between reward and cognitive control systems may be disrupted. In light of the results of our investigation, current theories of adolescent risk-taking should be refined to reflect that the disruption between reward and cognitive control systems is not apparent in all contexts, and reward can promote better cognitive control in adolescents. Reward-facilitated improvement of cognitive control, through an increase in sustained brain activation within the cognitive control network, is a process that appears to be continuous across development, from childhood to early adulthood. These findings will help researchers to refine theories on the neurobiological underpinnings of developmental changes in risk-taking. Identifying these neural mechanisms is a critical step in understanding and developing interventions for dangerous, risky behavior often exhibited by adolescents.

Conflict of interest

The authors declare no conflicts of interest.

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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.2014.07.005.

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