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PAPER

Adolescents let sufficient evidence accumulate before making a decision when large incentives are at stake

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Abstract

Adolescent decision-making has been described as impulsive and suboptimal in the presence of incentives. In this study we examined the neural substrates of adolescent decision-making using a perceptual discrimination task for which small and large rewards were associated with correctly detecting the direction of motion of a cloud of moving dots. Adults showed a reward bias of faster reaction times on trials for which the direction of motion was associated with a large reward. Adolescents, in contrast, were slower to make decisions on trials associated with large rewards. This behavioral pattern in adolescents was paralleled by greater recruitment of fronto-parietal regions important in representing the accumulation of evidence sufficient for selecting one choice over its alternative and the certainty of that choice. The findings suggest that when large incentives are dependent on performance, adolescents may require more evidence to accumulate prior to responding, to be certain to maximize their gains. Adults, in contrast, appear to be quicker in evaluating the evidence for a decision when primed by rewards. Overall these findings suggest that rather than reacting hastily, adolescents can be incentivized to take more time to make decisions when large rewards are at stake.

A video abstract of this article can be viewed at http://youtu.be/1g4F5vzFDl0

Introduction

As humans, we are forced to make thousands of simple and quite complex decisions each day. Optimal decision-making requires that we weigh prior knowledge with information in the present to arrive at an optimal decision. A number of factors influence decision-making such as the likelihood of a positive outcome following a particular choice. Given the heightened sensitivity to incentives during adolescence (Casey, Duhoux & Malter Cohen, 2010; Cohen, Asarnow, Sabb, Bilder, Bookheimer, Knowlton & Poldrack, 2010; Ernst, Nelson, Jazbec, McClure, Monk, Leibenluft, Blair & Pine, 2005; Galvan, Hare, Parra, Penn, Voss, Glover & Casey, 2006; Geier, Terwilliger, Teslovich, Velanova & Luna, 2010; Luna, 2009; Somerville & Casey, 2010; Somerville, Hare & Casey, 2011; van Leijenhorst, Zanolie, Van Meel, Westenberg, Rombouts & Crone, 2010) the current study examines how rewards influence adolescent decision-making and how this is represented in the underlying neural circuitry

Biasing of decisions with rewards is thought to involve dopamine-rich basal ganglia circuitry (Kawagoe, Takikawa & Hikosaka, 1998; Lau & Glimcher, 2008; Mogenson, Jones & Yim, 1980; Samejima, Ueda, Doya & Kimura, 2005; Satoh, Nakai, Sato & Kimura, 2003), where dopamine is released at the presentation of cues previously associated with rewards (Goto & Grace, 2005; Nicola, Taha, Kim & Fields, 2005; Phillips, Stuber, Heien, Wightman & Carelli, 2003). Adolescence is a period during which significant dopaminergic changes take place in the prefrontal cortex and nucleus accumbens (Kalsbeek, Voorn, Buijs, Pool & Uylings, 1988; Rosenberg & Lewis, 1994,1995; Tarazi, Tomasini &

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Baldessarini, 1998). Reward-based decisions during this period have been characterized by a tension between the development of 'bottom-up' striatal regions that express exaggerated reactivity to motivational stimuli and later-maturing 'top-down' cortical control regions (Casey, Getz & Galvan, 2008; Ernst, Pine & Hardin, 2006; Ernst, Romeo & Andersen, 2009; Geier & Luna, 2009; Steinberg, 2008). Presumably, this bottom-up system that has been associated with reward-seeking and risk-taking behavior gradually loses its competitive edge with the progressive emergence of 'top-down' regulation during development. With age and experience, the connectivity between these regions is strengthened and provides a mechanism for top-down modulation of the subcortically driven reward behavior (Somerville *et al.*, 2011; van den Bos, Cohen, Kahnt & Crone, 2012).

Although the majority of studies on adolescent decision-making have focused on suboptimal choices in the context of rewards (Figner, Mackinlay, Wilkening & Weber, 2009; Somerville *et al.*, 2011; Blakemore & Robbins, 2012), incentives can also enhance performance (Geier *et al.*, 2010). Suboptimal decisions typically occur in tasks with immediate reward conditions (Cauffman, Shulman, Steinberg, Claus, Banich, Graham & Woolard, 2010; Figner *et al.*, 2009; Steinberg, Graham, O'Brien, Woolard, Cauffman & Banich, 2009) or in tasks requiring suppression of an action toward cues previously associated with positive outcomes (Somerville *et al.*, 2011). In these cases, adolescents perform worse than both children and adults. This behavioral pattern is mirrored in ventral striatal activity, where adolescents show an increase in activation relative to children and adults to positive cues (Somerville *et al.*, 2011). Studies in which incentives have been shown to improve decision-making in adolescents have made the reward dependent upon accuracy in performance (Hardin, Mandell, Mueller, Dahl, Pine & Ernst, 2009; Jazbec, Hardin, Schroth, McClure, Pine & Ernst, 2006) or made the potential outcomes of choices known (Tymula, Rosenberg Belmaker, Roy, Ruderman, Manson, Glimcher & Levy, 2012). Reward-dependent improvements in behavior appear greater for adolescents than adults and are paralleled by heightened activation of both the ventral striatum and prefrontal regions during the preparation and execution of correct responses, suggestive of reward-related enhancement of control regions (Geier *et al.*, 2010). Thus, incentives yield better decision-making in adolescents when they are performance-dependent, but can hinder decision-making when used as distractors.

How rewards impact choices and actions across development has remained an area of increasing investigation. A recent approach for trying to understand the basis for these developmental effects has been to use probabilistic reward paradigms (Cohen *et al.*, 2010; van den Bos, Güroğlu, van den Bulk, Rombouts & Cone, 2009; van den Bos *et al.*, 2012). These studies examine how the expectations of receiving a reward based on prior outcomes and its value (e.g. low or high magnitude) impact future choices. Cohen and colleagues have shown that individuals are more accurate and quicker to react when responding to predictable stimuli. However, adolescents respond more quickly to stimuli that have been previously associated with a higher reward value. Adolescents also show greater ventral striatal activity to higher, unpredicted reward compared to adults and children. This heightened positive prediction error and striatal activity has been suggested as a possible mechanism for increased risky decisions during adolescence. Alternatively, Crone and colleagues (van den Bos *et al.*, 2012) have shown neural representation of prediction errors to be similar across age. According to their work, the functional connectivity between the ventral striatum and prefrontal cortex is what is changing as a function of age, consistent with earlier reports (Somerville *et al.*, 2011). As such, developmental changes in decision-making may not be related to differences in reward-related learning signals *per se* but rather in how these signals can guide behavior and expectations (van den Bos *et al.*, 2009, 2012). Thus at different ages, incentives and outcomes may drive behavior in different ways or lead to different decision-making strategies.

The current study tested how incentives may differentially impact decisions across development. A multitude of tasks have been used to examine the influence of reward on decisions in adolescents (Cauffman *et al.*, 2010; Figner *et al.*, 2009; Somerville *et al.*, 2011; Steinberg *et al.*, 2009). However, to understand the dynamics of decision-making, perceptual paradigms like the random-dot motion task (Britten, Shadlen, Newsome & Movshon, 1992) have been used to model the integration of information, i.e. sensory evidence, towards a decision threshold, or the point at which a decision is reached (Bogacz & Gurney, 2007; Lo & Wang, 2006; Smith & Ratcliff, 2004). Electrophysiological studies in nonhuman primates show that a decision is made once the firing of neurons in the dorsolateral prefrontal cortex (dlPFC) and the lateral intraparietal (LIP) cortex reach a given threshold (Hanes & Schall, 1996; Hanks, Ditterich & Shadlen, 2006; Huk & Shadlen, 2005; Kim & Shadlen, 1999). This increase in firing is assumed to represent the accumulation of evidence sufficient for selecting one choice over its alternatives. Recent human imaging studies have identified a similar frontal-parietal network using comparable decision-making tasks, specifically in the dlPFC and intraparietal sulcus (IPS), a homologue of the nonhuman primate LIP (Forstmann, Dutilh, Brown, Neumann, von Cramon,

Ridderinkhof & Wagenmakers, 2008; Heekeren, Marrett, Bandettini & Ungerleider, 2004; Ivanoff, Branning & Marois, 2008; Tosoni, Galati, Romani & Corbetta, 2008; van Veen, Krug & Carter, 2008).

Although variants of this task have been used with developmental populations (e.g. Mulder, Bos, Weusten, van Belle, van Dijk, Simen, van Engeland & Durston, 2010), few studies have included a reward manipulation with humans (Nagano-Saito, Cisek, Perna, Shirdel, Benkelfat, Leyton & Dagher, 2012). In the current study, we tested whether incentives bias perceptual decisions differentially across development while attempting to address nuisance factors that are inherent in many developmental studies. These nuisance factors include developmental differences in baseline performance and perceived salience of rewards. For example, studies showing greater improvement in performance in adolescents relative to adults, when performance is rewarded (e.g. Geier *et al*., 2010), have baseline performance nearer ceiling for the adults relative to the adolescents. Ceiling performance may limit the degree to which rewards can further facilitate performance and may obscure potential effects of incentives. Likewise, incentives may have different perceived value depending on age. For example, it has been shown that larger monetary rewards influence behavior more than smaller rewards (e.g. Galvan, Hare, Davidson, Spicer, Glover & Casey, 2005), and that adolescents are more sensitive to stimuli that have been associated with a high reward value relative to children and adults (Galvan *et al*., 2006, Cohen *et al*., 2010). Using money as an incentive may subjectively feel like a larger reward for an adolescent who typically has access to less money than an adult. Thus, developmental differences in performance, either diminished or enhanced, may be due to pre-existing differences in the value of incentives for one group relative to another in addition to differences in task difficulty.

In order to equate task difficulty, we used a variation of a random-dot motion discrimination task (Gold & Shadlen, 2001, 2002; Shadlen & Newsome, 2001) and parametrically titrated task difficulty by increasing or decreasing the amount of motion coherence of a cloud of randomly moving dots (Figure 1). We controlled for differences in difficulty between age groups by maintaining accuracy at 92% (easy condition) or 63% (hard condition) for each individual participant using a staircase function (King-Smith, Grigsby, Vingrys, Benes & Supowit, 1994; Watson & Pelli, 1983). We then added a reward component to the task using a point system as opposed to money or social cues in an attempt to eliminate potential developmental differences in the perceived value or salience of the reward. These manipulations provide an opportunity for testing the extent to which adolescent and adult decisions are differentially biased by incentives when decisions are difficult (e.g. low motion coherence) or easy (e.g. high motion coherence) and while controlling for differences between ages in reward value.

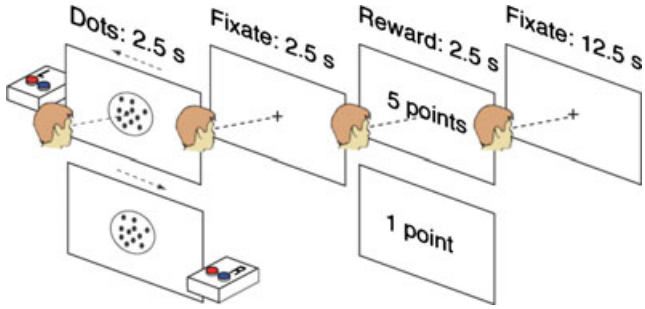

Figure 1 *Random-dot motion task with asymmetric rewards. Subjects were instructed to indicate the direction of random-dot motion with a button press. Figure adapted from Mulder et al., 2010.*

We hypothesized that trials associated with large rewards (5 points) would bias participants to respond more quickly, with adolescents showing a greater reward bias (Galvan *et al*., 2005, 2006; Cohen *et al*., 2010) and predicted that this behavioral pattern would be paralleled by increased activity in the ventral striatum to large reward trials (Galvan *et al*., 2005; Geier *et al*., 2010; Spicer, Galvan, Hare, Voss, Glover & Casey, 2007; Cohen *et al*., 2010). Finally, based on recent decision-making studies using performance-based reward with human adolescents (Geier *et al*., 2010) and adults (Nagano-Saito *et al*., 2012) and with nonhuman primates (Hanes & Schall, 1996; Hanks *et al*., 2006; Kim & Shadlen, 1999), we predicted that the amount of time or evidence needed to make a decision would be correlated with activity in decision-related fronto-parietal circuitry.

Methods

Participants

Forty-two right-handed subjects between the ages of 11 and 30 years participated in the fMRI experiment. Three subjects were excluded from analyses because of imaging artifacts. Another subject showed large lapses in performance, causing the staircase procedure used to maintain individual performance to fail, and was therefore also excluded. The remaining 38 subjects were divided into equal samples of those under 21 years (13 females; ages 11–20, mean = 15.84, *SD* = 2.06) and those 21 and over (nine females; ages 22–30, mean = 25.11, *SD* = 2.26). Subjects had no history of psychiatric or neurological disorder. Each participant gave informed consent or

assent, in the case of minors, according to procedures approved by the Institutional Review Board. A mock scanner was used to acclimate subjects to the scanner environment prior to the experiment.

Random-dot motion task

Subjects attended to a cloud of randomly moving white dots on a black background and decided which direction the dots were moving in by responding with a left or right button press. They were also informed that sometimes they would be awarded points for correct responses and to try to earn as many points as possible. Subjects were instructed to maintain fixation on the middle of the screen and respond to each trial as quickly but accurately as possible. The moving dots were presented for 2.5s followed by a delay of 2.5s, and then a feedback display was shown for 2.5s that consisted of a large reward (5 points), small reward (1 point), the word 'incorrect' for an error choice, or 'missed' for no response. The trial was then followed by an inter-trial interval of 12.5 sec of fixation (see Figure 1). Each subject performed 40 practice trials (~3 minutes) and 114 experimental trials, divided over 6 sessions (~6 minutes) of 19 trials each. During the practice trials, no reward manipulation was used and only feedback about a correct, incorrect, or missed trial was given.

The stimuli were generated on a Macintosh computer ('Mac-mini' 1.5 GHz PowerPC G4, Mac OS X 10.4.5) by using custom software (B. Heasley & J. Gold, Department of Neuroscience, University of Pennsylvania) and the Psychophysics Toolbox Version 3.0.8 (Brainard, 1997; Pelli, 1997) for Matlab (v7.3, Mathworks, MA). E-prime (Psychology Software Tools, Inc., Pittsburgh, PA) was used to control stimulus timing and response logging. E-prime was installed on the integrated functional imaging system (IFIS) (PST, Pittsburgh) with an LCD video display in the bore of the MR scanner and a fiber optic response collection device. The motion stimuli were similar to those used elsewhere (Britten *et al.*, 1992; Gold & Shadlen, 2003; Mulder *et al.*, 2010; Mulder, Wagenmakers, Ratcliff, Boekel & Forstmann, 2012; Newsome & Paré, 1988; Palmer, Huk & Shadlen, 2005; Ratcliff & McKoon, 2008): white dots, with a size of 3 × 3 pixels, moved within a circle with diameter of 6° with a speed of 5°/s and a density of 16.7 dots/deg^2/s on a black background.

Easy and difficult trials were pseudo-randomly divided over a total of 114 trials. Difficult trials were defined as the motion strength at which subjects performed at 63% accuracy. Easy trials were defined as the motion strength at 92% accuracy. Before the actual experiment started, 40 trials were acquired using a previously published adaptive psychometric algorithm to estimate the 63% and 92% performance levels (King-Smith *et al.*, 1994; Watson & Pelli, 1983). These motion strengths were used as starting points for each difficulty level. During the experiment, a staircase procedure was used to keep performance levels at 63% and 92% accuracy. There were 72 difficult and 44 easy trials, resulting in an equal total (~40) of correct trials for each level.

Large and small reward trials were pseudo-randomly divided over the 114 trials, such that 50% of the trials were paired with a large reward. Large reward was always associated with the same direction of motion for each subject and counterbalanced across subjects. To be consistent with nonhuman primate studies using this task (Gold & Shadlen, 2000), we did not inform participants of the contingency between the direction of motion and specific reward amount, nor was the trial preceded by a cue indicating the reward amount. On correct, large reward trials, subjects earned 5 points. On correct, small reward trials, subjects earned 1 point. Incorrect trials were followed by a display of the word 'incorrect' earning 0 points, missed trials (no response) were followed by the word 'miss' and no points were rewarded.

Behavioral data analysis

Behavioral data were analyzed using accuracy and latency to respond to the direction in which the dots were moving. Only correct trials were used and outliers were removed (reaction time scores 3 standard deviations above or below the individual's mean reaction time score). Within each subject, the reaction time for each trial was *z*-score transformed using that individual's mean reaction time and standard deviation. Gender was also entered into the model of all analyses due to the greater number of females in our sample. All reported ANOVAs and post-hoc *t*-tests were performed using IBM SPSS Statistics for Windows, Version 20.0.0 (Armonk, NY: IBM Corp).

Image acquisition

Imaging was performed using a 3T General Electric (Milwaukee, WI) MRI scanner using a quadrature head coil. Functional scans were acquired using a spiral in and out sequence (Glover & Thomason, 2004), where coronal slices were obliquely acquired anterior to posterior, resulting in partial brain volumes, from the frontal pole to posterior regions of the parietal lobe. The parameters were: repetition time (TR) = 2500 ms, echo time (TE) = 30 ms, 64 × 64 matrix, 34 4-mm coronal slices, 3.125 × 3.125 mm in-plane resolution, flip 90°, 155 repetitions were collected for each of the six test runs.

In addition, a high-resolution, T1-weighted anatomical scan (3D Magnetization Prepared Rapid Acquisition Gradient Echo [MPRAGE] 256 × 192 in-plane resolution, 240-mm FOV; 124 1.5-mm sagittal slices) was acquired for each subject and used to co-register and normalize functional images to the standard stereotaxic space using AFNI's automated Talairach Method of Piecewise Linear Scaling (TMPLS) (Cox, 1996) (Talairach Coordinate Space). Warping parameters were obtained from the transformation of each subject's high-resolution anatomical scan using a 12-parameter affine transformation to a template volume (TT_N27).

Imaging data processing

The fMRI data processing and analysis was performed using Analysis of Functional NeuroImages software (AFNI; Cox, 1996). Functional datasets were corrected for slice acquisition time and realigned within and across runs to correct for head motion. Motion parameters were estimated, and used in each subject's general linear model (GLM) as regressors of non-interest. Functional datasets were co-registered to each participant's high-resolution anatomical scan, converted to percent signal change, transformed into the standard coordinate space of Talairach and Tournoux (1988) and smoothed with a 4-mm FWHM Gaussian kernel.

Imaging data analysis

For each participant, a first-level voxel-wise parametrically modulated GLM was estimated. Regressors were created for each task condition (hard-large reward, hard-small reward, easy-large reward, easy-small reward) and convolved with a gamma-variate hemodynamic response function that contained the stimulus onset times for each trial-by-task condition, with a fixed duration of 7.5s that included the presentation of the moving dots (2.5s), delay (2.5s), and feedback (2.5s). Motion parameters, linear and quadratic trend for each run, trial-by-trial reaction times and error trials (comprising incorrect and missed trials) were modeled as regressors of non-interest. TRs with more than 1.56 mm motion displacement in any plane were omitted from GLM estimation using the 'censor' function in AFNI. In each case, less than 10% of the total functional data were excluded from the analyses. Of the 38 subjects, 17 (seven adults) had data excluded from the GLM due to excessive motion, however, within this subset, the amount of censoring between adolescents and adults did not differ ($t(15) = 0.51$, $p > .60$).

Two analyses were performed. First, given the literature and our hypotheses on reward and decision-related circuitry, a region of interest (ROI) analysis was performed using *a priori* defined ROIs of the ventral striatum (VS), dorsolateral prefrontal cortex (dlPFC) and intraparietal sulcus (IPS). These regions were identified using coordinates from a recent study of adults using similar reward manipulations and dot motion task (Nagano-Saito *et al.*, 2012). Coordinates were translated into Talairach-Tourneaux standard space and ROI masks were created as spheres around these coordinates with a radius of 4 mm, each containing seven 3 × 3 × 3 voxels. The following Talairach coordinates were used as the point of origin for each bilateral ROI: ventral striatum (±6,10,1), dorsolateral prefrontal cortex (±42,28,21), intraparietal sulcus (±42,−41,43). Parameter estimates were extracted for the four conditions for each participant from each ROI. A group ANOVA was conducted with within-subject factors of trial type (easy, hard) and reward (small, large) and between-subject factors of age group (adolescents, adults) and gender (male, female). Post-hoc *t*-tests were run to probe interactions that passed significance using the Hochberg-Benjamini procedure (1990) to control the false discovery rate of multiple comparisons at $p < .05$.

In addition, a whole-brain voxel-wise analysis was performed. Parameter estimate (β) maps for the conditions hard-large, hard-small, easy-large, and easy-small were carried to a random effects group analysis. A group linear mixed effects model was conducted with factors of trial type (within subjects: easy, hard), reward (within subjects: small, large) and group (between subjects: adolescents, adults). Resulting clusters considered statistically significant exceeded whole-brain correction for multiple comparisons using a *p*-value and cluster combination identified by Monte Carlo simulations using AFNIs 3DClustSim program (Ward, 2000) to preserve a corrected alpha < 0.05 unless otherwise specified (see Supplemental Table S1).

Results

Behavioral results

The mixed analysis of variance (ANOVA) with between-subject variables of age group (adolescents, adults) and gender (male, female) and within-subject variables of difficulty (easy, hard) and reward (small or large) on mean accuracy showed a main effect of difficulty of $F(1, 34) = 413.87$, $p < .00001$, but no other effects or interactions. This main effect confirms that our staircase procedure, used to maintain difficulty at 'easy' (92% accuracy) or 'hard' (63% accuracy) levels, was successful. Moreover, we successfully controlled performance across

age groups as evidenced by no interaction of age group × difficulty ($F(1, 34) = 0.00$, $p < .99$). Further, there were no significant differences between adolescents and adults in mean motion coherence for the hard condition, (12% (*SD* = 11%) and 12% (*SD* = 15%), $p < .91$) and only a trend in the easy condition (47% (*SD* = 18%) and 36% (*SD* = 18%), $p = .059$).

A mixed analysis of variance (ANOVA) with between-subject variables of age (adolescents, adults) and gender (male, female) and within-subject variables of difficulty (easy, hard) and reward (small, large) on normalized reaction time (*z*-scores) showed a main effect of difficulty ($F(1, 34) = 38.53$, $p < .0001$) and interactions of difficulty × reward ($F(1, 34) = 5.77$, $p < .02$), and age group × reward (Figure 2; $F(1, 34) = 4.14$, $p < .05$). The main effect of difficulty on response latency further validates our difficulty manipulations, with longer reaction times for hard (*M* = 1420 ms, *SD* = 230) relative to easy trials (*M* = 1266 ms, *SD* = 207).

The difficulty × reward interaction was driven by faster responses for large reward trials (*M* = 1240 ms; *SD* = 210) relative to small reward trials (*M* = 1295 ms; *SD* = 226) ($t(37) = 2.54$, $p < .02$, paired *t*-test of *z*-scored RTs) for the easy condition, but not the hard condition ($p > .57$, paired *t*-test of *z*-scored RTs).

Of greatest interest is the reward × age group interaction depicted in Figure 2. This interaction is driven by a reward bias in adults as evidenced by faster reaction times on large reward trials, relative to adolescents who were slower to make a decision when a large reward was at stake ($t(36) = 2.25$, $p < .04$). Conversely, when smaller rewards were at stake, adults took longer to respond than adolescents ($t(36) = 2.64$, $p < .02$), consistent with the adults showing a classic reward bias (faster to large rewards) and the adolescents showing the inverse pattern. These effects were apparent in easy trials early in the task (run 1) in adults ($t(18) = 2.810$, $p < .012$) with faster RTs to large reward trials relative to small, and by the middle of the experiment (run 4 of 6) in adolescents ($t(16) = -3.355$, $p < .004$), who exhibited slower RTs to large reward relative to small.

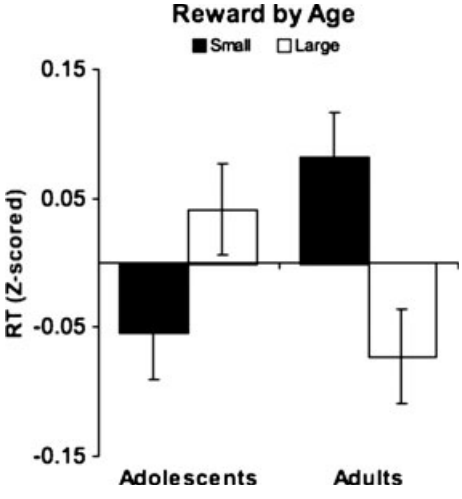

Figure 2 *Reward by age interaction in response time. Behavioral plot of reward by age interaction, average z-transformed reaction times.*

To examine whether the age × reward interaction was driven more by the younger or older adolescents, we subdivided our under-21 age group and compared those individuals 11–15 years ($n = 9$, six females, mean = 14.22 (1.4 *SD*)) and those 16–20 years ($n = 10$, seven females, mean = 17.3 (1.4 *SD*) to those 21 and over. An age (young adolescents, older adolescents, adults) × reward interaction approached significance ($F(2, 32)$ $F = 2.79$, $p < .08$) and showed that although the younger adolescents slowed more on large reward trials relative to small reward trials, they did not significantly differ from older adolescents ($t(17) = 0.368$, $p > .71$) (see Supplemental Figure S2).

Imaging results

A 2 (Age Group: adolescents, adults) × 2 (Gender: male, female) × 2 (Reward level: small, large) × 2 (Difficulty level: easy, hard) analysis of variance (ANOVA) was conducted within each of three *a priori* defined ROIs (ventral striatum, dlPFC, IPS) to identify regions differentially activated by task conditions and age group with particular emphasis on the behavioral interaction of age × reward. Post-hoc *t*-tests were then performed to probe any significant interactions using a Hochberg-Benjamini (1990) procedure to correct for multiple comparisons.

Ventral striatum

A main effect of reward ($F(1, 34) = 10.00$, $p < .003$) was seen in the ventral striatum with greater activity for large relative to small reward trials (Figure 3), but there was no age × reward interaction ($p > .94$).

Intraparietal sulcus

A main effect of age ($F(1, 34) = 8.74$, $p < .006$) and reward × age interaction ($F(1, 34) = 6.67$, $p < .014$) were observed in the IPS (Figure 4). The main effect of age revealed greater activity in this region for adolescents than adults. The interaction of age × reward also showed greater IPS activity to large reward trials in adolescents relative to adults ($t(36) = 2.58$, $p < 0.014$). To test whether the age × reward interaction was driven more by the younger or older adolescents, we split them into

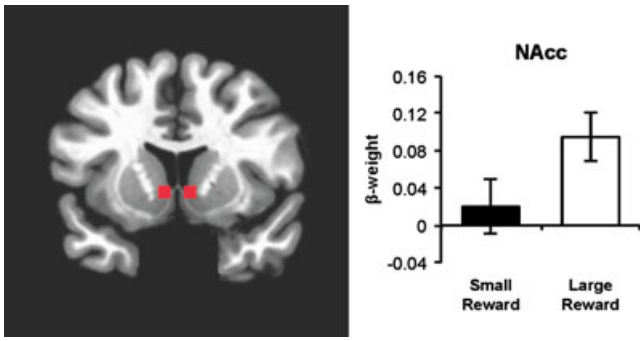

Figure 3 *Main effect of reward in the ventral striatum. Left: A priori defined region of interest in the ventral striatum used for analyses. Region of interest mask is rendered on a representative high-resolution anatomical scan Right: Plot of activity in the ventral striatum by reward valence. NAcc = nucleus accumbens.*

two subgroups identical to the behavioral analysis. The age group (early- and late-adolescents, adults) × reward interaction did not reach significance ($F(2, 32) = 3.23$, $p < .06$), but suggested that although the older adolescents had slightly greater IPS activity than the younger adolescents on large reward trials relative to small, they did not significantly differ ($t(17) = -0.098$, $p > .92$; Supplemental Figure S2).

Dorsolateral prefrontal cortex

Consistent with the IPS, an age × reward interaction was seen in the dlPFC (Figure 4, F(1, 34) = 6.17, $p < .018$). Similar to the pattern seen in the IPS, there was a trend in activation, where adolescents showed greater recruitment of dlPFC during large reward trials, compared to their adult counterparts ($t(36) = 1.93$, $p < .062$). Again, to confirm the age × reward effect was not disproportionally driven by a subgroup of the adolescents, we tested for early- and late-adolescence effects. The age group (early- and late-adolescents, adults) × reward interaction did not reach significance ($F(2, 32) = 3.18$, $p < .06$) and dlPFC activity on large reward trials relative to small was not significantly different between the younger and older adolescent groups ($t(17) = 0.20$, $p > .84$; Supplemental Figure S2).

Whole-brain analysis

A whole-brain voxel-wise ANOVA was conducted to identify additional regions of interest (see Supplemental Figure S1). A main effect of difficulty (hard versus easy trials) was seen in basal ganglia thalamocortical circuitry that included bilateral inferior frontal gyrus (IFG), thalamus and striatum, as well as the dorsal anterior cingulate. All regions were differentially engaged as a function of difficulty, showing significantly greater responses to 'hard' relative to 'easy' trials (see Supplemental Table S1). Regions identified for the main effect of reward included the ventral and dorsal anterior cingulate cortex, right thalamus, right inferior frontal gyrus ($p < .05$, whole-brain corrected) and bilateral ventral striatum ($p < .05$, uncorrected). All regions showed greater activity for large relative to small reward trials. Similar to our ROI analysis, a main effect of reward was observed in the ventral striatum, and age × reward interactions were seen in bilateral dlPFC and IPS ($p < .05$, uncorrected, see Supplemental Table S1).

Functional connectivity

To further interrogate the age × reward interaction, a psychophysiological interaction (PPI) analysis was performed using the ventral striatum ROI as a seed-point to determine whether brain regions were temporally correlated on the large relative to small reward trials for each age group separately. This analysis identified regions of right IPS (36, −44, 33) and bi-lateral dlPFC (Right: 25,

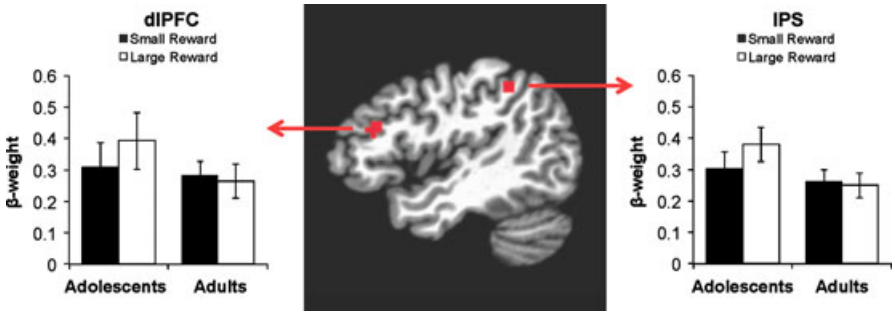

Figure 4 *Age × reward interactions in fronto-parietal regions. Left: BOLD activity in dlPFC as a function of reward and age group ($p < .018$, corrected). Middle: A priori defined regions of interest in the dlPFC and IPS used for analyses. Region of interest masks are rendered on a representative high-resolution anatomical scan. Right: BOLD activity in IPS as a function of reward and age group ($p < .017$, corrected). dlPFC = dorsolateral prefrontal cortex; IPS = intraparietal sulcus.*

28, 32; Left: −28, 28, 32) ($p < .05$, uncorrected) for adults, but not adolescents. The adult findings are consistent with the ventral striatum modulating decision-making circuitry that is also reflected by faster reaction times on large reward trials.

Discussion

Our findings suggest that when large incentives are at stake, adolescents, relative to adults, may require or allow greater time for sufficient evidence to accumulate before making a decision. This behavior is paralleled by increased activation of fronto-parietal circuitry, in the dlPFC and IPS, regions important in representing the accumulation of evidence prior to selecting one choice from alternative ones (Forstmann *et al.*, 2008; Heekeren *et al.*, 2004; Ivanoff *et al.*, 2008; Tosoni *et al.*, 2008; van Veen *et al.*, 2008). Thus, even when equating task difficulty and using points as incentives, we see differences in decision behavior and in the brain between adolescents and adults.

These results indicate that the use of incentives – as simple as accruing points for correct performance – was an effective and 'salient' manipulation for both age groups in terms of altering decision behavior, but in different ways. Whereas adults showed a bias toward the direction of motion associated with a large reward (i.e. faster reaction times), adolescents showed slower reaction times for these trials. Our use of a point system was an attempt to employ a reward of similar familiarity and salience across ages. One index of reward salience often used in imaging studies is ventral striatal activity (Cooper & Knutsen, 2008). In adolescents, this activity is typically elevated for monetary and social rewards relative to children and adults (Galvan *et al.*, 2006, Geier *et al.*, 2010; van Leijenhorst *et al.*, 2010; Somerville *et al.*, 2011; Cohen *et al.*, 2010). However, when using points in the current study, we saw similar ventral striatal activity in adolescents and adults and no interaction of age group by reward, suggestive of similar perceived value of the points. This finding may suggest that previous studies showing heightened ventral striatal activity in adolescence to reward cues relative to adults may have been due to differences in perceived value of the rewards. Nonetheless, we cannot rule out the possibility of developmental differences in the motivation level induced by simply earning points. Clearly, equating motivation and reward salience across ages is a challenge that remains for developmental studies.

Unlike previous versions of the moving dots task, in the current task reward level was purposefully asymmetric. Specifically, the direction of motion associated with a large reward was consistent throughout the task for each participant. This consistency in the association between large reward and direction of moving dots may have led adults to use a strategy or be primed to respond to the direction associated with larger reward. However, if this were the case, one might expect to see more false alarms in the direction associated with large reward. Yet accuracy and motion coherence were similar across age groups. In monkeys, correlates of the biasing influence of asymmetric rewards on response latencies have been found in areas of parietal and prefrontal cortex (Coe, Tomihara, Matsuzawa & Hikosaka, 2002; Ding & Hikosaka, 2006; Leon & Shadlen, 1999; Platt & Glimcher, 1999) similar to our results.

Age differences in decision-making and brain activity are unlikely to be due to differences in baseline performance or perceptual ability since difficulty level and accuracies were controlled in this experiment. Rather, they appear to be due to a differential response to incentives. Specifically, our findings suggest that if a large incentive is at stake, adolescents, relative to adults, allow greater time for sufficient evidence to accumulate before making a decision to ensure that they get the outcome of 5 points as opposed to nothing. Consistent with this finding is recent economic theory-based behavioral findings (Tymula *et al.*, 2012) that show that adolescents are less risky than adults in their choices when the outcomes are certain. In the current experiment the outcomes were certain in that subjects quickly learned which direction of motion was associated with a large reward, and that they would lose that reward if they were incorrect.

Our behavioral findings are constrained by our imaging results that show greater activity in IPS in adolescents than in adults on high reward trials. Electrophysiological studies in LIP, the nonhuman primate homologue of the IPS, show that a decision is made once the firing of neurons in this area reaches a given threshold (Hanes & Schall, 1996; Hanks *et al.*, 2006; Huk & Shadlen, 2005; Kim & Shadlen, 1999). This increase in firing is assumed to represent the accumulation of evidence sufficient for selecting one choice over its alternatives. More recently the firing rate of LIP neurons has been shown not only to correlate with selecting a choice, but also with the degree of certainty in that choice (Kiana & Shadlen, 2009). Thus, our findings of heightened IPS activity and longer response times on high reward trials in adolescents relative to adults suggest that adolescents were allowing sufficient evidence to accumulate to be certain of the accuracy of their choice before making a response when 5 points were at stake.

The question remains as to why incentives would modulate behavior differently for adolescents and adults. A recent explanation suggested by van den Bos and

colleagues (2012) is that reward values and learning signals impact less mature decision-related frontostriatal (Liston, Watts, Tottenham, Davidson, Niogi, Ulug & Casey, 2006; Somerville *et al*., 2011) and fronto-parietal (Fair, Dosenbach, Church, Cohen, Brahmbhatt, Miezin, Barch, Raichle, Petersen & Schlaggar, 2007; Klingberg, Forssberg & Westerberg, 2002; Olesen, Nagy, Westerberg & Klingberg, 2003; van den Bos *et al*., 2009) circuitry differently from mature circuitry. Our functional connectivity results are consistent with this interpretation in that we showed evidence of coupling between the ventral striatum and bilateral prefrontal and parietal regions that was not apparent in adolescents. The lack of functional coupling among these regions in adolescents may be consistent with less ability to efficiently modulate this circuitry in the immature brain (van den Bos *et al*., 2012), as evidenced in slower reaction times on large reward trials by the adolescents.

Unlike most studies of adolescence that focus on the teenage years, the current study focused on differences between individuals under 21 relative to those 21 and older. Although this age range is broad, it may be justified in light of significant changes in brain structure (Gogtay, Geidd, Lusk, Hayashi, Greenstein, Vaituzis, Nugent, Herman, Classen, Toga, Rapoport & Thompson, 2004) and increase in risk taking (National Research Council, 2011) that occur into the twenties, and given that individuals under 21 have not acquired all their legal rights in the US and are considered minors in government-regulated research. Nonetheless, to understand when during development our results were most evident, we subdivided our adolescent sample into those under and over 16 years of age. Comparing the younger and older youths relative to adults, we showed slightly longer reaction times and enhanced IPS activity on large reward trials relative to small reward trials in the youngest subjects. However, these two groups did not significantly differ from one another and neither of these groups showed a flip in their pattern of responding that adults showed, of faster reaction times on large reward trials (see Supplemental Figure S2).

It should be noted that due to the task design, namely the lack of variable-length inter-stimulus intervals between trial events, we were unable to model the decision, response and outcome separately. Thus we cannot specifically link our findings to initial or subsequent decision thresholds. Furthermore, this design may have prevented us from observing developmental differences in ventral striatal activity to large rewards. However, we do show an age × reward interaction in behavior that occurs prior to reward outcome, and is paralleled in the dlPFC and IPS, regions shown in nonhuman primate studies to be involved in representing accumulation of evidence for one choice relative to another (Hanes & Schall, 1996; Huk & Shadlen, 2005; Kim & Shadlen, 1999). Moreover, as reaction time was treated as a covariate in our imaging analysis, we show that these findings are not simply due to longer response times associated with developmental differences in simple perceptual or motor abilities. Nonetheless, we cannot directly link the observed greater fronto-parietal activity in adolescents relative to adults to the specific decision process of accumulating evidence.

In conclusion, this study shows that reward magnitude differentially alters decision-making in adolescents and adults. Rather than reacting hastily, adolescents take more time to make decisions when large incentives are at stake. This behavioral pattern is paralleled by an increase in fronto-parietal activity in adolescence relative to adults. This circuitry has been shown to represent the accumulation of evidence sufficient for selecting one choice over its alternative and in the certainty of that choice in nonhuman primate studies (Hanes & Schall, 1996; Hanks *et al*., 2006; Kim & Shadlen, 1999; Kiana & Shadlen, 2009). Continued development of this circuitry throughout adolescence (Fair *et al*., 2007; Klingberg *et al*., 2002; Olesen *et al*., 2003) may lead to differences in how incentives can modulate decisions in adolescents relative to adults (van den Bos *et al*., 2009, 2012). Our findings contribute to a growing literature on adolescent decision-making and have important implications for how to slow down otherwise impulsive choices and actions by using performance-based incentives.

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References

Blakemore, S.J., & Robbins, T.W. (2012). Decision-making in the adolescent brain. *Nature Neuroscience*, **15** (9), 1184–1191.

Bogacz, R., & Gurney, K. (2007). The basal ganglia and cortex implement optimal decision making between alternative actions. *Neuralal Computation*, **19**, 442–477.

Brainard, D.H. (1997). The Psychophysics Toolbox. *Spatial Vision*, **10** (4), 433–436.

Britten, K.H., Shadlen, M.N., Newsome, W.T., & Movshon, J.A. (1992). The analysis of visual motion: a comparison of neuronal and psychophysical performance. *Journal of Neuroscience*, **12**, 4745–4765.

Casey, B.J., Duhoux, S., & Malter Cohen, M. (2010). Adolescence: what do transmission, transition, and translation have to do with it? *Neuron*, **67** (5), 749–760.

Casey, B.J., Getz, S., & Galvan, A. (2008). The adolescent brain. *Developmental Review*, **28** (1), 62–77.

Cauffman, E., Shulman, E.P., Steinberg, L., Claus, E., Banich, M.T., Graham, S.J., & Woolard, J. (2010). Age differences in affective decision making as indexed by performance on the Iowa Gambling Task. *Developmental Psychobiology*, **46** (1), 193–207.

Coe, B., Tomihara, K., Matsuzawa, M., & Hikosaka, O. (2002). Visual and anticipatory bias in three cortical eye fields of the monkey during an adaptive decision-making task. *Journal of Neuroscience*, **22** (12), 5081–5090.

Cohen, J.R., Asarnow, R.F., Sabb, F.W., Bilder, R.M., Bookheimer, S.Y., Knowlton, B.J., & Poldrack, R.A. (2010). A unique adolescent response to reward prediction errors. *Nature Neuroscience*, **13** (6), 669–671.

Cooper, J.C., & Knutsen, B. (2008). Valence and salience contribute to nucleus accumbens activation. *NeuroImage*, **39** (1), 538–547.

Cox R.W. (1996). AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, **18**, 1973–1983.

Ding, L., & Hikosaka, O. (2006). Comparison of reward modulation in the frontal eye field and caudate of the macaque. *Journal of Neuroscience*, **26** (25), 6695–6703.

Ernst, M., Nelson, E.E., Jazbec, S., McClure, E.B., Monk, C.S., Leibenluft, E., Blair, J., & Pine, D.S. (2005). Amygdala and nucleus accumbens in responses to receipt and omission of gains in adults and adolescents. *NeuroImage*, **25** (4), 1279–1291.

Ernst, M., Pine, D.S., & Hardin, M. (2006). Triadic model of the neurobiology of motivated behavior in adolescence. *Psychological Medicine*, **36** (3), 299–312.

Ernst, M., Romeo, R.D., & Andersen, S.L. (2009). Neurobiology of the development of motivated behaviors in adolescence: a window into a neural systems model. *Pharmacology, Biochemistry and Behavior*, **93** (3), 199–211.

Fair, D., Dosenbach, N.U., Church, J.A., Cohen, A.L., Brahmbhatt, S., Miezin, F.M., Barch, D.M., Raichle, M.E., Petersen, S.E., & Schlaggar, B.L. (2007). Development of distinct control networks through segregation and integration. *Proceedings of the National Academy of Sciences, USA*, **104** (33), 13507–13512.

Figner, B., Mackinlay, R.J., Wilkening, F., & Weber, E.U. (2009). Affective and deliberative processes in risky choice: age differences in risk taking in the Columbia Card Task. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **35**, 709–730.

Forstmann, B., Dutilh, G., Brown, S., Neumann, J., von Cramon, D.Y., Ridderinkhof, K.R., & Wagenmakers, E.J. (2008). Striatum and pre-SMA facilitate decision-making under time pressure. *Proceedings of the National Academy of Sciences, USA*, **105**, 17538–17542.

Galvan, A., Hare, T.A., Davidson, M., Spicer, J., Glover, G., & Casey, B.J. (2005). The role of ventral frontostriatal circuitry in reward-based learning in humans. *Journal of Neuroscience*, **25**, 8650–8656.

Galvan, A., Hare, T.A., Parra, C.E., Penn, J., Voss, H., Glover, G., & Casey, B.J. (2006). Earlier development of the accumbens relative to orbitofrontal cortex might underlie risk-taking behavior in adolescents. *Journal of Neuroscience*, **26**, 6885–6892.

Geier, C.F., & Luna, B. (2009). The maturation of incentive processing and cognitive control. *Cerebral Cortex*, **20** (7), 1613–1629.

Geier, C.F., Terwilliger, R., Teslovich, T., Velanova, K., & Luna, B. (2010). Immaturities in reward processing and its influence on inhibitory control in adolescence. *Cerebral Cortex*, **20** (7), 1613–1629.

Glover, G., & Thomason, M. (2004). Improved combination of spiral-in/out images for BOLD fMRI. *Magnetic Resonance in Medicine: Official Journal of the Society of Magnetic Resonance in Medicine / Society of Magnetic Resonance in Medicine*, **51** (4), 863–868.

Gogtay, N., Geidd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzis, A.C., Nugent, T.F. 3rd, Herman, D.H., Classen, L.S., Toga, A.W., Rapoport, J.L., & Thompson, P.M. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences, USA*, **101** (21), 8174–8179.

Gold, J.I., & Shadlen, M.N. (2000). Representation of a perceptual decision in developing oculomotor commands. *Nature*, **404**, 390–394.

Gold, J.I., & Shadlen, M.N. (2001). Neural computations that underlie decisions about sensory stimuli. *Trends in Cognitive Sciences*, **5** (1), 10–16.

Gold, J.I., & Shadlen, M.N. (2002). Banburismus and the brain: decoding the relationship between sensory stimuli, decisions, and reward. *Neuron*, **36** (2), 299–308.

Gold, J.I., & Shadlen, M.N. (2003). The influence of behavioral context on the representation of a perceptual decision in developing oculomotor commands. *Journal of Neuroscience*, **23**, 632–651.

Goto, Y., & Grace, A.A. (2005). Dopaminergic modulation of limbic and cortical drive of nucleus accumbens in goal-directed behavior. *Nature Neuroscience*, **8**, 805–812.

Hanes, D.P., & Schall, J.D. (1996). Neural control of voluntary movement initiation. *Science*, **274**, 427–430.

Hanks, T.D., Ditterich, J, & Shadlen, M.N.(2006). Microstimulation of macaque area LIP affects decision-making in a motion discrimination task. *Nature Neuroscience*, **9**, 682–689.

Hardin, M.G., Mandell, D., Mueller, S.C., Dahl, R.E., Pine, D.S., & Ernst, M.(2009). Inhibitory control in anxious and healthy adolescents is mo dulated by incentive and incidental affective stimuli. *Child Psychology and Psychiatry*, **50**, 1550–1558.

Heekeren, H.R., Marrett, S., Bandettini, P.A., & Ungerleider, L.G. (2004). A general mechanism for perceptual decision-making in the human brain. *Nature*, **431** (7010), 859–862.

Hochberg, Y., & Benjamini, Y. (1990). More powerful procedures for multiple significance testing. *Statistics in Medicine*, **9** (7), 811–818.

Huk, A.C., & Shadlen, M.N. (2005). Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *Journal of Neuroscience*, **25** (45), 10420–10436.

Ivanoff, J., Branning, P., & Marois, R. (2008). fMRI evidence for a dual process account of the speed–accuracy tradeoff in decision-making. *PLoS One*, **3**, e2635.

Jazbec, S., Hardin, M.G., Schroth, E., McClure, E., Pine, D.S., & Ernst, M. (2006). Age-related influence of contingencies on a saccade task. *Experimental Brain Research*, **174**, 754–762.

Kalsbeek, A., Voorn, P., Buijs, R.M., Pool, C.W., & Uylings, H.B. (1988). Development of the dopaminergic innervation in the prefrontal cortex of the rat. *Journal of Comparative Neurology*, **269** (1), 58–72.

Kawagoe, R., Takikawa, Y., & Hikosaka, O. (1998). Expectation of reward modulates cognitive signals in the basal ganglia. *Nature Neuroscience*, **1** (5), 411–416.

Kiana, R., & Shadlen, M.N. (2009). Representation of confidence associated with a decision by neurons in the parietal cortex. *Science*, **324** (5928), 759–764.

Kim, J.N., & Shadlen, M.N. (1999). Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nature Neuroscience*, **2** (2), 176–185.

King-Smith, P.E., Grigsby, S.S., Vingrys, A.J., Benes, S.C., & Supowit, A. (1994). Efficient and unbiased modifications of the QUEST threshold method: theory, simulations, experimental evaluation and practical implementation. *Vision Research*, **34** (7), 885–912.

Klingberg, T., Forssberg, H., & Westerberg, H. (2002). Increased brain activity in frontal and parietal cortex underlies the development of visuospatial working memory capacity during childhood. *Journal of Cognitive Neuroscience*, **14** (1), 1–10.

Lau, B., & Glimcher, P.W. (2008). Value representations in the primate striatum during matching behavior. *Neuron*, **58**, 451–463.

Leon, M.I., & Shadlen, M.N. (1999). Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. *Neuron*, **24** (2), 415–425.

Liston, C., Watts, R., Tottenham, N., Davidson, M.C., Niogi, S., Ulug, A.M., & Casey, B.J. (2006). Frontostriatal microstructure modulates efficient recruitment of cognitive control. *Cerebral Cortex*, **16** (4), 553–560.

Lo, C.C., & Wang, X.J. (2006). Cortico-basal ganglia circuit mechanism for a decision threshold in reaction time tasks. *Nature Neuroscience*, **9**, 956–963.

Luna, B. (2009). Developmental changes in cognitive control through adolescence. *Advances in Child Development and Behavior*, **37**, 233–278.

Mogenson, G.J., Jones, D.L., & Yim, C.Y. (1980). From motivation to action: functional interface between the limbic system and the motor system. *Progress in Neurobiology*, **14**, 69–97.

Mulder, M.J., Bos, D., Weusten, J.M., van Belle, J., van Dijk, S.C., Simen, P., van Engeland, H., & Durston, S. (2010). Basic impairments in regulating the speed–accuracy tradeoff predict symptoms of attention-deficit/hyperactivity disorder. *Biological Psychiatry*, **68**, 1114–1119.

Mulder, M.J., Wagenmakers, E.J., Ratcliff, R., Boekel, W., & Forstmann, B.U. (2012). Bias in the brain: a diffusion model analysis of prior probability and potential payoff. *Journal of Neuroscience*, **32** (7), 2335–2343.

Nagano-Saito, A., Cisek, P., Perna, A.S., Shirdel, F.Z., Benkelfat, C., Leyton, M., & Dagher, A. (2012). From anticipation to action, the role of dopamine in perceptual decision-making: an fMRI-tyrosine depletion study. *Journal of Neurophysiology*, **108** (2), 501–512.

National Research Council (2011). *The science of adolescent risk-taking: Workshop report*. Washington, DC: The National Academies Press.

Newsome, W.T., & Paré, E.B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, **8** (6), 2201–2211.

Nicola, S.M., Taha, S.A., Kim, S.W., & Fields, H.L. (2005). Nucleus accumbens dopamine release is necessary and sufficient to promote the behavioral response to reward-predictive cues. *Neuroscience*, **135**, 1025–1033.

Olesen, P., Nagy, Z., Westerberg, H., & Klingberg, T. (2003). Combined analysis of DTI and fMRI data reveals a joint maturation of white and grey matter in a fronto-parietal network. *Cognitive Brain Research*, **18** (1), 48–57.

Palmer, J., Huk, A.C., & Shadlen, M.N. (2005). The effect of stimulus strength on the speed and accuracy of a perceptual decision. *Journal of Vision*, **5** (5), 376–404.

Pelli, D.G. (1997). The Video Toolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, **10** (4), 437–442.

Phillips, P.E., Stuber, G.D., Heien, M.L., Wightman, R.M., & Carelli, R.M. (2003). Subsecond dopamine release promotes cocaine seeking. *Nature*, **422**, 614–618.

Platt, M.L., & Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. *Nature*, **400** (6741), 233–238.

Ratcliff, R., & McKoon, G. (2008). The diffusion decision model: theory and data for two-choice decision tasks. *Neural Computation*, **20**, 873–922.

Rosenberg, D.R., & Lewis, D.A. (1994). Changes in the dopaminergic innervation of monkey prefrontal cortex during late postnatal development: a tyrosine hydroxylase immunohistochemical study. *Biological Psychiatry*, **36** (4), 272–277.

Rosenberg, D.R., & Lewis, D.A. (1995). Postnatal maturation of the dopaminergic innervation of monkey prefrontal and motor cortices: a tyrosine hydroxylase immunohistochemical analysis. *Journal of Comparative Neurology*, **358** (3), 383–400.

Samejima, K., Ueda, Y., Doya, K., & Kimura, M. (2005). Representation of action-specific reward values in the striatum. *Science*, **310**, 1337–1340.

Satoh, T., Nakai, S., Sato T., & Kimura, M. (2003). Correlated coding of motivation and outcome of decision by dopamine neurons. *Journal of Neuroscience*, **23**, 9913–9923.

Shadlen, M.N, & Newsome, W.T. (2001). Neural basis of a decision in the parietal cortex (area LIP) of the rhesus monkey. *Journal of Neurophysiology*, **86** (4), 1916–1936.

Smith, P.L., & Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends in Neurosciences*, **27** (3), 161–168.

Somerville, L.H., & Casey, B.J. (2010). Developmental neurobiology of cognitive control and motivational systems. *Current Opinion in Neurobiology*, **20** (2), 236–241.

Somerville, L.H., Hare, T., & Casey, B.J. (2011). Frontostriatal maturation predicts cognitive control failure to appetitive cues in adolescents. *Journal of Cognitive Neuroscience*, **23** (9), 2123–2134.

Spicer, J., Galvan, A., Hare, T.A., Voss, H., Glover, G., & Casey, B.J. (2007). Sensitivity of the nucleus accumbens to violation in expectation of reward. *NeuroImage*, **34** (1), 455–461.

Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review*, **28** (1), 78–106.

Steinberg, L., Graham, S., O'Brien, L., Woolard, J., Cauffman, E., & Banich, M. (2009). Age differences in future orientation and delay discounting. *Child Development*, **80**, 28–44.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain* (M. Rayport, trans). New York: Thieme.

Tarazi, F.I., Tomasini, E.C., & Baldessarini, R.J. (1998). Postnatal development of dopamine and serotonin transporters in rat caudate-putamen and nucleus accumbens septi. *Neuroscience Letters*, **254** (1), 21–24.

Tosoni, A., Galati, G., Romani, G.L., & Corbetta, M. (2008). Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nature Neuroscience*, **11**, 1446–1453.

Tymula, A., Rosenberg Belmaker, L.A., Roy, A.K., Ruderman, L., Manson, K., Glimcher, P.W., & Levy, I. (2012). Adolescents' risk-taking behavior is driven by tolerance to ambiguity. *Proceedings of the National Academy of Sciences, USA*, **109** (42), 17135–17140.

van den Bos, W., Cohen, M.X., Kahnt, T., & Crone, E.A. (2012). Striatum-medial prefrontal cortex connectivity predicts developmental changes in reinforcement learning. *Cerebral Cortex*, **22** (6), 1247–1255.

van den Bos, W., Güroğlu, B., van den Bulk, B.G., Rombouts, S.A.R.B., & Cone, E.A. (2009). Better than expected or as bad as you thought? The neurocognitive development of probabilistic feedback processing *Frontiers in Human Neuroscience*, **3**, 52.

van Leijenhorst, L., Zanolie, K., Van Meel, C.S., Westenberg, P.M., Rombouts, S.A., & Crone, E.A. (2010). What motivates the adolescent? Brain regions mediating reward sensitivity across adolescence *Cerebral Cortex*, **20** (1), 61–69.

van Veen, V., Krug, M.K., & Carter, C.S. (2008). The neural and computational basis of controlled speed–accuracy tradeoff during task performance. *Journal of Cognitive Neuroscience*, **20**, 1952–1965.

Ward, B.D. (2000). Simultaneous inference for fMRI data. From: http://afni.nimh.nih.gov/afni/doc/manual/AlphaSim.

Watson, A.B., & Pelli, D.G. (1983). QUEST: a Bayesian adaptive psychometric method. *Perception & Psychophysics*, **33** (2), 113–120.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Summary of imaging results from whole-brain analyses. All results exceed a p-value/cluster size combination ($p < .01/45$ voxels) that corresponds to whole-brain $p < .05$, corrected for multiple comparisons as calculated with Monte Carlo simulations in AFNI (3dClustSim), except for the main effect of difficulty, where a p-value/cluster size combination of $p < .0005/10$ voxels is used to distinguish subclusters within larger functional activations (>1000 voxels).

Fig S1 Main effect of difficulty. Brain regions showing differential activity as a function of difficulty (hard > easy). Activations, thresholded at $p < .05$, whole brain corrected, are rendered on a representative high-resolution anatomical scan. Slices were selected ($z = -30, -10, 0, 10, 20, 30$) to highlight the basal ganglia thalamocortical circuit.

Fig S2 Age by reward interaction in brain and behavior. Top: Behavioral plot of difference score between large and small reward trials across early-adolescents (11–15), late-adolescents (16–20) and adults (21 and up); average z-transformed reaction times. Middle: BOLD activity in dlPFC as a function of large reward bias and age group. Bottom: BOLD activity in IPS as a function of reward bias and age group. dlPFC = dorsolateral prefrontal cortex; IPS = intraparietal sulcus