Developmental Cognitive Neuroscience 2 (2012) 437–447

Contents lists available at SciVerse ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: http://www.elsevier.com/locate/dcn

Developmental effects of decision-making on sensitivity to reward: An fMRI study

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ARTICLE INFO

Article history:
Received 10 January 2012
Received in revised form 23 April 2012
Accepted 24 April 2012

Keywords:
Reward
Incentive
Brain
fMRI
Development
Adolescents
Decision-making

ABSTRACT

Studies comparing neural correlates of reward processing across development yield inconsistent findings. This challenges theories characterizing adolescents as globally hypo- or hypersensitive to rewards. Developmental differences in reward sensitivity may fluctuate based on reward magnitude, and on whether rewards require decision-making. We examined whether these factors modulate developmental differences in neural response during reward anticipation and/or receipt in 26 adolescents (14.05 ± 2.37 yrs) and 26 adults (31.25 ± 8.23 yrs). Brain activity was assessed with fMRI during reward anticipation, when subjects made responses with–vs.–without decision-making, to obtain large–vs.–small rewards, and during reward receipt. When reward-receipt required decision-making, neural activity did not differ by age. However, when reward receipt did not require decision-making, neural activity varied by development, reward magnitude, and stage of the reward task. During anticipation, adolescents, but not adults, exhibited greater activity in the insula, extending into putamen, and cingulate gyrus for large–vs.–small incentives. During feedback, adults, but not adolescents, exhibited greater activity in the precuneus for large–vs.–small incentives. These data indicate that age-related differences in reward sensitivity cannot be characterized by global hypo- or hyper-responsivity. Instead, neural responding in striatum, prefrontal cortex and precuneus is influenced by both situational demands and developmental factors. This suggests nuanced maturational effects in adolescent reward sensitivity.

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1. Introduction

Adolescent risky behavior may reflect immature brain function (Ernst and Fudge, 2009). Developmental theories suggest that such immaturity may result in global reward-related hypo- (e.g., Spear, 2000) or hypersensitivity (e.g., Ernst and Hardin, 2009; Somerville et al., 2010). However, inconsistent findings from imaging studies suggest more nuanced maturational effects in adolescent reward sensitivity (Bjork et al., 2010; Ernst and Fudge, 2009; Geier and Luna, 2009; Geier et al., 2010; Steinberg, 2008). As such, variability in task design may contribute to inconsistencies in existing brain-imaging research on adolescent reward processing.

One task feature that differs across existing studies is whether reward receipt depends on a subject's decisions. Paradigms without decision-making (e.g., Bjork et al.,

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1878-9293/$ – see front matter. Published by Elsevier Ltd.
http://dx.doi.org/10.1016/j.dcn.2012.04.002

2004, 2010; van Leijenhorst et al., 2010b) require subjects to execute a pre-specified response (e.g., press button 1) to obtain a reward. In paradigms that require decision-making (e.g., Cohen et al., 2010; Ernst et al., 2005; Eshel et al., 2007; Forbes et al., 2010; van Leijenhorst et al., 2010a), subjects must typically choose one of two possible responses (e.g., choose button 1 or 2). The present study considers whether such decision-making differentially influences neural sensitivity to incentive value in adults and adolescents during both reward anticipation and receipt. Neuroimaging studies assessing developmental differences in reward processing utilize paradigms that differ in their use of decision-making. Thus, it is critical to test directly if this aspect of task design influences outcomes.

While poor decision-making is often viewed as normative in adolescence, there is little evidence that adolescents are in fact deficient in the reasoning skills needed to make sound decisions (Furby and Beyth-Marom, 1992). For example, adolescents perform as well as adults when estimating their vulnerability to negative outcomes, or weighing the costs of risky behavior (for reviews, see Reyna and Farley, 2006; Steinberg, 2007). This suggests that adolescents possess the skills to make sound decisions, even if they fail to draw on these skills as consistently as adults.

Indeed, current developmental theories propose that adults, relative to adolescents, are more likely to employ top-down processes, which refer to processes that are goal-driven, and require considerable attention and cognitive control. In contrast, adolescents, relative to adults, are more likely to engage bottom-up processes, which are processes that are driven by stimulus features, such as high salience due to affective content. This dichotomy likely reflects the relative dominance of saliency-driven over goal-driven behavior in adolescents, despite the integrity of top-down processes in this age group (e.g., Ernst et al., 2011; Ernst and Fudge, 2009; Smith et al., 2011; Steinberg, 2007). Stimuli acquire salience by affective, motivational, and attention-based processes, which are mediated by dorsal anterior cingulate (dACC) and insular cortex (Habas et al., 2009; Seeley et al., 2007; Sridharan et al., 2008). Top-down processes that rely on executive control require engagement of distinct networks encompassing dorsolateral, dorsomedial, and ventrolateral prefrontal cortices (Funahashi, 2001; Miller and Cohen, 2001; Seeley et al., 2007; Venkatraman et al., 2009). One prediction that emerges from these theories is that cues signaling the need for decision-making necessarily engage top-down processes and thus minimize developmental differences in the circuitry engaged. In contrast, when reward-motivated behavior is executed without explicit engagement of decision-making, greater developmental disparities are expected due to greater influences from stimulus saliency, and thus incentive value, in adolescents relative to adults.

Decision-making refers to the selection of an option among a set of alternatives. Any decision-making involves a number of cognitive processes, such as discriminative attention, value appraisal, formation of a preference, and action execution (Ernst and Paulus, 2005). Even the most elementary choice, such as the choice between two simple options (press button 1 or button 2), engages these cognitive processes. Guessing is another example of decision-making, where individuals select an option based primarily on "gut feelings". In contrast, instrumental responding, which is guided far less heavily by the manifestation of a preference (e.g., press a button as fast as possible), requires minimal levels of decision-making. The cognitive processes engaged by decision-making are executive functions that rely on prefrontal neural circuitry and modulate subcortical activity (Elliott et al., 1999; Han et al., 2009; Lau et al., 2004). Thus, given our specific interest in developmental differences in the neural circuitry mediating response to incentives, and the influence of cognitive control on this response, we examine neural responses to reward anticipation in both the presence and absence of simple decision-making.

Importantly, it remains unknown whether developmental differences in reward processing emerge as a function of decision-making. Developmental studies of reward processing use experimental paradigms in which incentives are obtained *either* with *or* without decision-making; no study directly contrasts these two classes of events. In addition, distinct cognitive processes engaged during reward anticipation vs. receipt may modulate age-specific effects on decision-making. For instance, on tasks that require decision-making, there are developmental differences in dACC (Eshel et al., 2007; van Leijenhorst et al., 2010a) and orbitofrontal cortex (Eshel et al., 2007) activation during reward anticipation, but only in striatal activity during reward receipt (Ernst et al., 2005; Forbes et al., 2010; van Leijenhorst et al., 2010a). Conversely, on tasks that do not require decision-making, there are developmental differences in the insular cortex (Bjork et al., 2010) and striatum (Bjork et al., 2004, 2010) during reward anticipation, but no developmental differences during reward receipt (Bjork et al., 2004, 2010). Finally, reward magnitude may further impact these developmental differences (Bjork et al., 2004; Galvan et al., 2006; van Leijenhorst et al., 2010a). Indeed, few studies investigate developmental differences in neural sensitivity to large and small incentives, either during reward anticipation or reward receipt.

The current study addresses a growing need to test the effect of key task parameters on developmental differences in brain function during reward processing. If task parameters modulate developmental differences in reward processing, cross-study differences in these parameters could generate the inconsistent results found among existing neuroimaging studies. Moreover, much like the existing inconsistencies in the published literature, direct observation of such task-related modulation in a single study would challenge theories attributing global differences in reward function to adolescents and adults. The current study compares neural activity in adults and adolescents while they complete a reward paradigm that manipulates whether decision-making is required to obtain large and small incentives (Bar-Haim et al., 2009; Helfinstein et al., 2011). We predict that, within each stage of reward processing, development will modulate neural activity based

Table 1
Mean (SD) demographic characteristics for adolescents and adults.

	Adolescents	Adults
Sex (female/male)	13/13	15/11
Age	14.05 (2.37)	31.25 (8.23)
SES	37.64 (15.09)	44.00 (15.24)
IQ	112.96 (13.85)	119.16 (10.18)

on incentive value and on whether decision-making is required. For rewards obtained without decision-making, and thus with minimal top-down processing, we predict that adolescents will exhibit greater activity than adults for large, compared with small, incentives in brain regions that process stimulus salience, such as dACC and anterior insula, as well as in regions sensitive to incentive value, such as striatum. For rewards obtained with decision-making, we predict that developmental differences for large, compared with small, incentives will be minimized, due to the necessary, overt engagement of top-down processes.

2. Materials and methods

2.1. Subjects

Informed consent from 38 adults, and assent with parental consent from 48 adolescents, was obtained prior to participation in this National Institute of Mental Health Institutional Review Board approved study. The current analysis included 26 adults and 26 adolescents (Table 1). A subset of adolescents were excluded for excessive head motion ($\geq$3 mm; $N = 13$), technical difficulties ($N = 7$), excessive signal dropout ($N = 2$), or having siblings in the study ($N = 2$). Adolescents excluded based on excessive motion tended to be younger than those without excessive motion, but only marginally so ($M = 12.43$ yrs, SD = 2.84; $p = .07$). A subset of adults were excluded for excessive head motion ($N = 3$), technical difficulties ($N = 3$), or excessive signal dropout ($N = 6$). Subjects had no past or current history of psychiatric disorder, as determined by Structured Clinical Interview for DSM-IV (First et al., 2002) in adults, or Schedule for Affective Disorders and Schizophrenia for School Aged Children (Kaufman et al., 1997) in adolescents. Groups did not differ by gender, socioeconomic status (Hollingshead, 1975), or IQ (Weschler, 1999).

2.2. Reward processing task

Subjects were told they could win points and earn up to $25 by completing a task designed to assess neural activity during the anticipation and receipt of rewards (Fig. 1A) (Bar-Haim et al., 2009; Helfinstein et al., 2011). Each point was equivalent to 10¢. To minimize potential developmental differences in monetary valuation, subjects were not specifically informed of the point-to-money conversion rate. For each trial, subjects were asked to provide the correct response to a visual cue. After a variable inter-stimulus interval, subjects learned whether they received a reward for their response.

2.2.1. Anticipation

Each trial began with an anticipation event (1500 ms), during which a colored circle (cue) prompted subjects to provide a button press (1 or 2). Cue color indicated the type of trial (choice, no-choice, motor), while the cue size indicated the incentive size of potential reward (small: 3-points, large: 6-points). For no-choice trials, "1" or "2" appeared within the cue, directing subjects to press the corresponding button to gain points. For choice trials, "?" appeared within the cue, prompting subjects to choose the correct response to gain points. For motor trials, a blank cue prompted subjects to press any button, with no opportunity to gain points. Thus, the task included five types of anticipation events, reflecting choice and no-choice events with small and large potential rewards, and a non-rewarded motor event.

2.2.2. Receipt

During receipt events (1000 ms), subjects learned whether they had obtained a reward, and their total points. Unbeknownst to subjects, half of their choice responses were randomly selected to result in reward, and half to result in omission of reward. No-choice responses, when performed correctly, always resulted in reward. No-choice response errors (i.e., subject presses a button other than the one specified within the cue) resulted in omission of reward. Motor trials did not involve a receipt event. The task therefore included six types of reward receipt events, reflecting receipt of small and large rewards obtained with or without choice, and omission of small and large rewards from choice events.

2.2.3. Jitter

Jitter was introduced via the presentation of a purple rectangle (1000 ms), which was an incidental stimulus that required no response. In rapid-event tasks such as the current one, jitter has become a standard approach to account for the refractory period associated with the hemodynamic response function (Dale, 1999; Huettel and McCarthy, 2000). Particularly for developmental studies such as this one, that rely on long, fatiguing tasks, jitter allows for deconvolution of complex events without adding the time required for slow-event-related designs. Here, incidental stimuli, which are often presented during jitter (Dale, 1999; Huettel and McCarthy, 2000), were identical to those used with by Tricomi et al. (2004). These incidental stimuli occurred randomly throughout the task. A variable number of incidental stimuli occurred between anticipation and receipt events (inter-stimulus interval = 0–4000 ms; 0–4 events; $M = 2000$ ms), and between trials (inter-trial interval = 0–2000 ms; 0–2 events; $M = 1000$ ms). Variable-duration jitter allowed neural response to anticipation and receipt events to be de-convolved independently. Presentation of incidental stimuli during jitter more finely controls for the visual aspects of other trials, relative to the "blank" trials or "fixation-crosses" used in some studies (Tricomi et al., 2004). Here, the overall duration of the jitter resulted in "null" events being present for approximately the same amount of time as events of interest. This ratio increases the ability to detect BOLD signal response

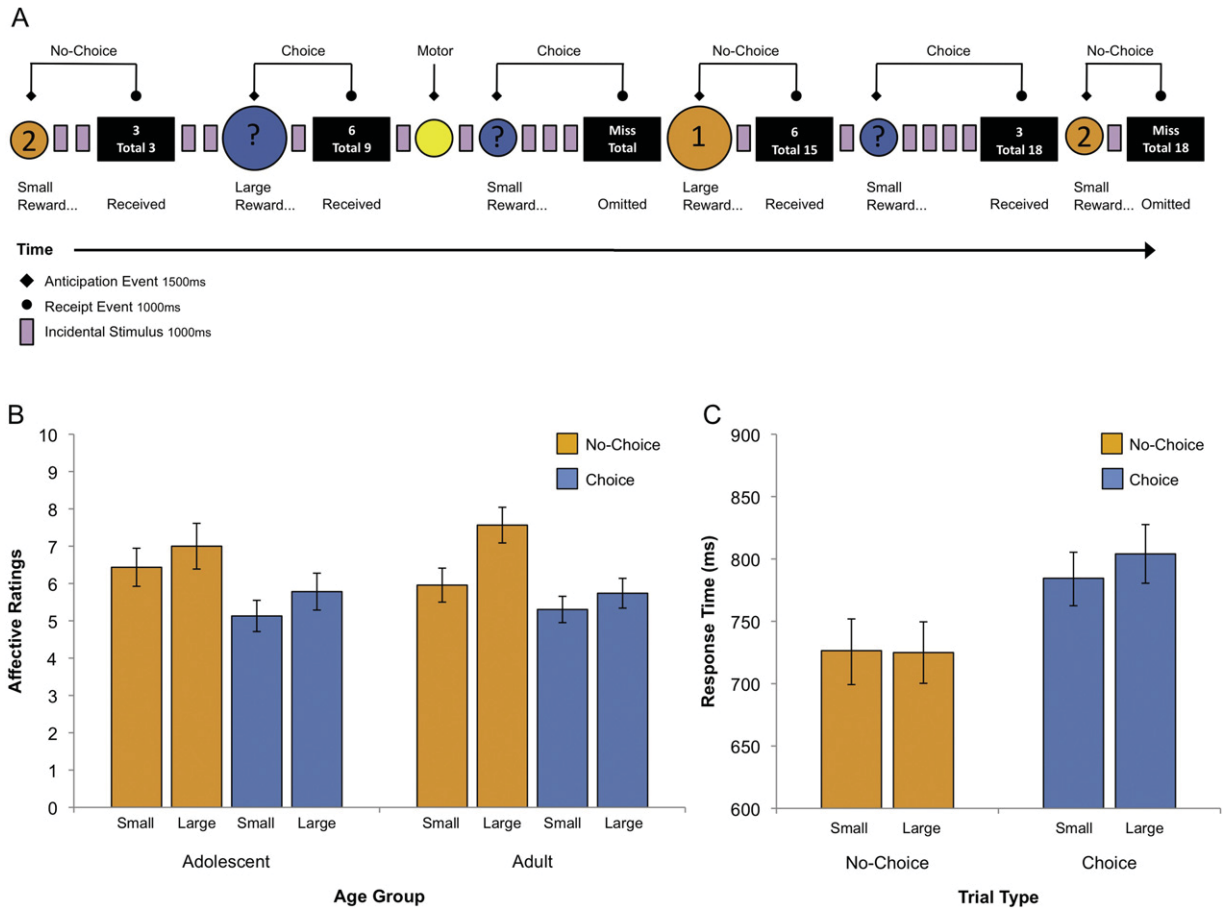

Fig. 1. Reward task design; results of self-report and behavioral data. (A) Each trial was comprised of reward anticipation (1500 ms) and receipt (1000 ms) stages. During reward anticipation, colored circle cues prompted subjects to respond. Cue color indicated the type of trial (no-choice: orange; choice: blue; motor: yellow). Size of no-choice and choice trials cues reflected incentive size (small: 3-points; large: 6-points). For no-choice trials, a "1" or "2" within the cue directed subjects to press the corresponding button to gain points. For choice trials, a "?" within the cue prompted subjects to guess the correct response to gain points. For motor trials, a small blank cue prompted subjects to press any button, with no opportunity to gain points. During reward receipt, subjects learned if their response was rewarded and their cumulative score. Incidental stimuli (1000 ms) were purple rectangles that introduced variable-duration jitter into the design, and required no response. Cue color was counterbalanced across subjects. Graphs depict average (±SEM) for (B) post-scan affective ratings, and (C) response times, for no-choice (orange) and choice (blue) trials.

to active events (Birn et al., 2002; Dale and Buckner, 1997).

2.2.4. Task comprehension and presentation

Adolescents and adults practiced, and successfully completed, several trials of the task prior to entering the scanner. After practicing, subjects were shown each type of cue, and were asked to describe the relationship between their response to each cue and potential reward outcomes. All subjects accurately reported that responses on no-choice trials would be rewarded if performed correctly, choice trials would be rewarded only if they selected the correct response, and that motor trials would not result in reward. After the scan was completed, subjects were asked again to describe the relationship between their response to each type of cue and reward outcomes, and again were able to describe this relationship accurately. The fact that all subjects were able to do this without difficulty suggests that the task was developmentally appropriate for the adolescents in the study. Once in the scanner, subjects completed three runs of 40 randomly presented trials (trials-per-run: choice = 16, no-choice = 16, motor = 8). This resulted in 48 choice, 48 no-choice, and 24 motor trials. The 5 anticipation and 6 receipt events yielded 11 trial-specific events. Cue color cue was counterbalanced across subjects. The E-Prime (Version 1.1; Psychology Software Tools, Inc.) program was presented via back-projection. Subjects responded via a hand-held two-button box (Cedrus Corporation).

2.3. Self-report measures

Immediately after scanning, subjects rated whether they thought the reward outcomes of the choice trials were rigged, or "fixed," by the experimenter (1–10: Not at all true–Very true). Subjects then rated their affect toward each of the 5 cues (1–10: Like–Dislike).

2.4. Imaging data acquisition

Neuroimaging data were acquired with a GE Signa, 3T-scanner (Waukesha, WI). For each subject, 495 functional images (165 per-run) with 30 contiguous 4 mm thick sagittal slices (in-plane resolution = 3.75 × 3.75 mm) were acquired using a T2*-weighted echo-planar sequence (TR/TE = 2500/23 ms, flip = 90°; FOV = 240 mm, matrix = 64 × 64). To facilitate anatomical localization and coregistration of functional data, a high-resolution structural scan was acquired (sagittal plane) with a T1-weighted magnetization-prepared spoiled gradient-recalled echo sequence (TR/TE = 8100/32 ms, flip = 15°; FOV = 240 mm, matrix = 256 × 256, in-plane resolution, 0.86 × 0.86 mm).

2.5. Data analysis

2.5.1. Self-report

Independent samples *t*-tests assessed whether adults and adolescents were equally unaware that reward outcomes for choice trials were computer-determined. A repeated-measures ANOVA was performed on affective ratings of reward cues, with two within-subject factors (decision-making [no-choice vs. choice]; incentive size [small vs. large]) and one between-subjects factor (age group [adult vs. adolescent]).

2.5.2. Behavior

Response time was assessed for choice and no-choice responses. After removing outliers (i.e., trials with response time > $M \pm 2.5$ SDs), a repeated-measures ANOVA was performed on response time, with two within-subject factors (decision-making [no-choice vs. choice] and incentive size [small vs. large]) and one between-subjects factor (age group [adult vs. adolescent]).

2.5.3. Imaging

Analysis of functional and neural images (AFNI; version 2.56b); (Cox, 1996) was used to preprocess and analyze imaging data. We implemented the same analytic path and exclusionary criteria for motion as prior studies using this paradigm (Bar-Haim et al., 2009; Helfinstein et al., 2011). Functional data were corrected for slice timing and registered to the high-resolution structural scan. Functional data were smoothed (6 mm kernel), spatially normalized, and resampled, resulting in 3.75 mm^3 voxels.

A random-effects analysis was conducted with a two-level procedure. Subject-level data were analyzed using multiple-regression. Task-specific regressors modeled each of the 5 anticipation events (no-choice$_{small}$, no-choice$_{large}$, choice$_{small}$, choice$_{large}$, motor), and each of the 6 feedback events (*reward:* no-choice$_{small}$, no-choice$_{large}$, choice$_{small}$, choice$_{large}$; *reward omission:* choice$_{small}$, choice$_{large}$). Although motor anticipation, non-rewarded choice events, and the few incorrectly performed no-choice events were modeled, they were not included in the present analyses. Incidental stimuli, included to introduce jitter, were not modeled.

Task-specific regressors were convolved with a gamma-variate basis function approximating the BOLD response (Cohen, 1997). Additional regressors modeled motion residuals and baseline drift. For each subject, this analysis produced a β-coefficient and associated *t*-statistic for each voxel and regressor. Percent signal change maps were generated by dividing signal intensity at each voxel by the mean voxel intensity for each run, and multiplying by 100.

Group-level analyses tested whether decision-making (no-choice vs. choice) and incentive size (small vs. large) moderated age group differences in neural activation during each processing stage (reward anticipation vs. receipt). Hypotheses were tested with two ANOVA models, which included two within-subjects factors (decision-making [no-choice vs. choice] and incentive size [small vs. large]), and one between-subjects factor (age group [adult vs. adolescent]). One model assessed brain activity during anticipation. The second model, which assessed brain activity during receipt, only included reward trials. This was because a primary goal of the study, i.e., contrasting activity during choice and no-choice events, can only be accomplished by comparing rewarded trials, since no-choice events did not result in reward omission. This particular analytic strategy was selected to match the design features of the experiment and the hypotheses that the study intended to address. This study was designed specifically to assess age-related modulation of the effects of decision-making and incentive magnitude on brain function. Thus, we conducted a 3-way ANOVA with age-group as the between-subjects factor, and decision-making and incentive size as the within-subjects factors, and selectively examined the brain regions that were modulated by the 3-way interaction.

Additional secondary analyses were conducted, beyond this primary analysis and its focus on a 3-way interaction (see Supplementary materials). These secondary analyses enhanced interpretation and placed the current findings in the context of other research. Specifically, these analyses contrasted each anticipation event of interest (no-choice$_{small}$, no-choice$_{large}$, choice$_{small}$, choice$_{large}$) and each receipt event of interest (*reward:* no-choice$_{small}$, no-choice$_{large}$, choice$_{small}$, choice$_{large}$), with implicit baseline, separately for adolescents and adults. Analyses were performed to confirm that the relatively simple decisions prompted by choice cues were sufficient to engage brain regions typically associated with top-down processing. To do this, across all subjects, anticipation events for choice (choice$_{small}$ + choice$_{large}$) were contrasted with anticipation events for no-choice (no-choice$_{small}$ + no-choice$_{large}$). Analyses were also performed to test for the effects of age on decision-making. This was tested with two ANOVA models, which included one within-subjects factor of decision-making (no-choice vs. choice), and one between-subjects factor of age group (adult vs. adolescent). One model assessed brain activity during anticipation. The second model, which assessed brain activity during receipt, only included reward trials.

The primary hypotheses were tested with a three-way interaction in each model. All analyses used a voxel-wise threshold of $p < .005$ with a 10-voxel extent threshold. Of note, this combination of threshold parameters yields a desirable balance between Type I and Type II error rate (Lieberman and Cunningham, 2009). In this instance, such

a balance is important because it allows a thorough exploration of the influence of complex tasks on brain activity in regions often excluded from developmental studies of reward processing. Of note, our study focuses on between-group differences in higher-order interactions, so balancing Type I and Type II error rates is essential. For clusters exhibiting significant three-way interactions, subject-level percent signal-change values were extracted and plotted to facilitate interpretation.

3. Results

3.1. Self-report

3.1.1. Awareness of computer-determined reward outcomes

Adults ($M = 2.26$, SD = 1.60) and adolescents ($M = 2.17$, SD = 1.99) were equally unaware that choice outcomes were computer-determined ($t < .5$, p = ns).

3.1.2. Affective ratings for reward cues (Fig. 1B)

There was a 3-way (age group × decision-making × incentive size) interaction for affective ratings of reward cues ($F(1, 44) = 4.44$, $p < .05$). Among adults, a decision-making × incentive size interaction ($F(1, 22) = 13.59$, $p = .001$) revealed that no-choice trials with large incentives were rated more positively than those with small incentives ($t(22) = 4.69$, $p < .001$). Incentive size did not influence adult ratings for choice trials ($t < 2$, p = ns). In adolescents, there was no decision-making-by-incentive size interaction ($F < 1$, p = ns), nor were there main effects of decision-making ($F < 4$, p = ns), or incentive size ($F < 3$; p = ns).

3.2. Behavioral response time (Fig. 1C)

The 3-way (age group × decision-making × incentive size) repeated measures ANOVA for response time was not significant ($F < 1$, p = ns). Thus, group did not influence in-scanner behavior. Nevertheless, while response time did not vary by age group, there was a decision-making × incentive size interaction ($F(1, 50) = 6.25$, $p < .05$), as well as a main effect of decision-making ($F(1,50) = 18.79$, $p < .001$) and incentive size ($F(1, 50) = 4.86$, $p < .05$). This indicated that regardless of age group, response time was slower for choice vs. no-choice trials ($t(51) = 1.99$, $p = .05$), and for large vs. small incentives ($t(51) = 3.91$, $p < .001$). However, the large compared with small incentive difference occurred only for choice ($t(51) = 3.02$, $p < .005$) but not no-choice, trials ($t < .50$, p = ns). Thus, reaction time varied as a function of both within-subject task-related parameters.

3.3. Imaging results

3.3.1. Anticipation

(Fig. 2; Table 2A): In four key regions, the 3-way (age group × decision-making × incentive size) repeated-measures ANOVA revealed significant 3-way interactions with large effect sizes (partial $\eta^2 > 0.1379$; Cohen, 1973). These regions included the right anterior insula extending into the putamen, left anterior insula, dACC, and mid-cingulate cortex (all p's < .005; see Table 2A for partial η^2 and F-values). In each instance, the three-way interaction reflected a decision-making × incentive size interaction in adolescents (all p's < .01; see Table 2A for F-values) but not adults (all p's > 10; see Table 2A for F-values).

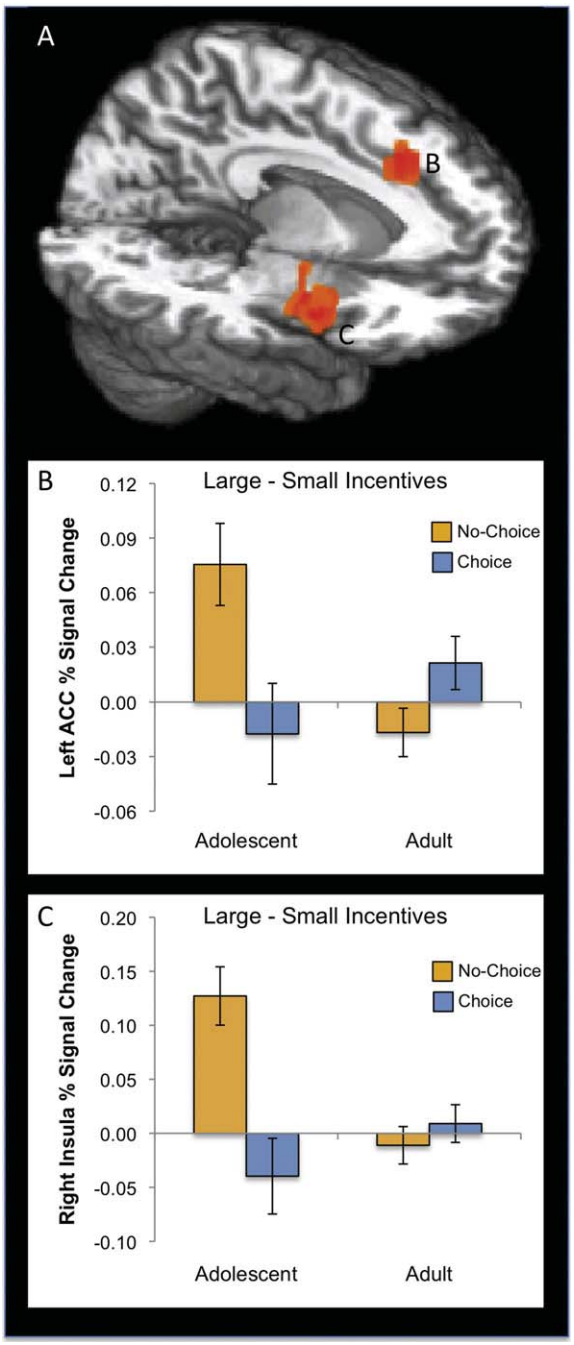

Fig. 2. Reward anticipation. (A) 3-way (age group x decision-making x incentive size) interaction found in insula extending to putamen, and dACC (MNI X-plane = 7; Z-plane = −4). Graphs depict this interaction. Bars represent mean (±SEM) percent signal change for large versus small incentives, during no-choice (orange) and choice (blue) reward anticipation in (B) right insula extending to striatum, and (C) right dACC.

Table 2
Activation clusters identified in 3-way interaction: Age (adult vs. adolescent) × decision-making (no-choice vs. choice) × incentive size (small vs. large).

Region	Peak MNI coordinates			Cluster size	Partial η^2	Age × decision × size	Adolescents: decision × size	Adults: decision × size
	x	*y*	*z*					
A. Anticipation						F^{***}	F^{**}	$F^{\S}$
Insula	−37	0	4	12	0.19	11.56	9.47	2.61
	34	8	−3	48	0.25	14.36	17.92	0.80
Cingulate	−7	22	43	14	0.19	11.63	8.43	3.18
	0	−17	40	11	0.18	11.70	7.84	3.50
B. Receipt						F^{***}	$F^{\S}$	F^{***}
Precuneus	−37	−68	33	48	0.09	17.86	1.73	12.17

** All *p*'s < .001.
*** All *p*'s < .005.
§ All *p*'s > .10.

In adolescents, the effect of incentive size on neural response was greater during no-choice than choice trials (see Fig. 2). Specifically, adolescents had greater activity in these regions for large compared with small incentives in the no-choice trials (all *t*'s > 3.30; all *p*'s < .005), and exhibited no incentive-related difference on choice trials (all *t*'s < 1.50; all *p*'s > .25).

3.3.2. Receipt

(Fig. 3; Table 2B): The 3-way (age group × decision-making × incentive size) repeated-measures ANOVA revealed a significant 3-way interaction, here with a medium effect size (partial $\eta^2 > 0.0588$; Cohen, 1973). This interaction emerged only in the left precuneus ($p < .005$; see Table 2B for partial η^2 and *F*-value). In direct contrast with the results during anticipation, the three-way interaction reflected a decision-making × incentive size interaction in adults ($p < .005$; see Table 2B for *F*-value) but not adolescents ($p > .10$; see Table 2B for *F*-value). In adults, the effect of incentive size on neural response was greater during no-choice than choice trials (see Fig. 3). Specifically, adults had greater activity for large compared with small incentives in the no-choice trials ($t = 3.01$; $p < .01$), with no difference in choice trials ($t = -.84$, $p > .40$).

3.3.3. Secondary analyses (Supplementary Materials)

Secondary analyses indicate that, when compared with an implicit baseline, each anticipation event of interest ($\text{no-choice}_{\text{small}}$, $\text{no-choice}_{\text{large}}$, $\text{choice}_{\text{small}}$, $\text{choice}_{\text{large}}$) elicited extensive activity among adolescents and adults in regions including striatum, insula, and anterior cingulate (see Supplementary Figs. 1 and 2; Tables 1–8). In addition to this pattern of activation, both adolescents and adults exhibited deactivation in medial prefrontal cortex and posterior cingulate, primarily during choice trials. Secondary analyses also confirm that, compared with no-choice events ($\text{no-choice}_{\text{small}} + \text{no-choice}_{\text{large}}$), choice events ($\text{choice}_{\text{small}} + \text{choice}_{\text{large}}$) during anticipation elicit extensive activity in regions typically associated with top-down processing, including dorsomedial and dorsolateral prefrontal cortex (see Supplementary Fig. 3; Table 9). During anticipation there was no age group × decision-making interaction in the brain. During receipt there was an age group × decision-making interaction in inferior parietal lobule (41, -48, 27; 108 voxels).

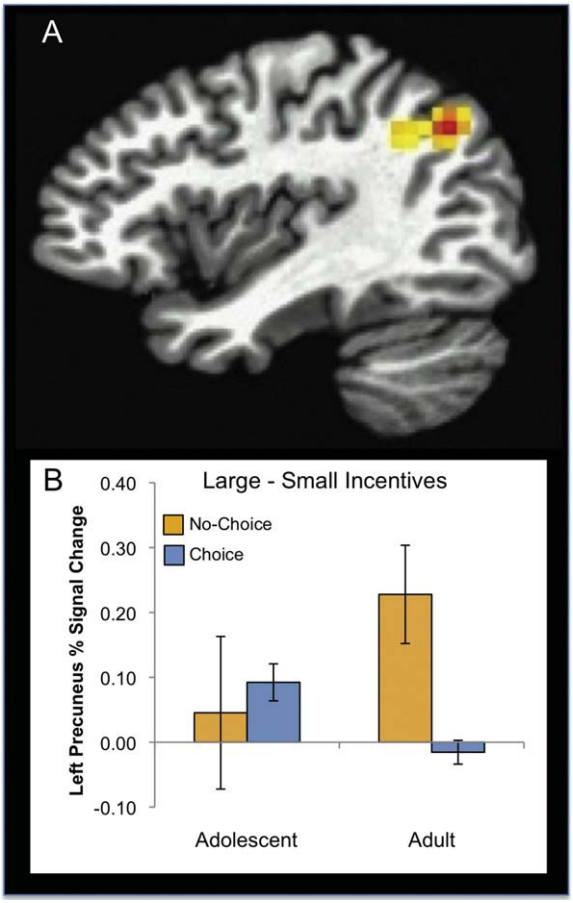

Fig. 3. Reward receipt. (A) 3-way (Age X Decision-making X Incentive size) interaction found in precuneus (MNI X-plane = −37). Graph depict this interaction. Bars represent mean (±SEM) percent signal change for large versus small incentives, during no-choice (orange) and choice (blue) reward receipt in (B) left precuneus.

4. Discussion

This is the first study to show that the need to engage even simple decision-making processes in order to obtain rewards differentially influences neural sensitivity to incentives in adolescents and adults. These data suggest that developmental differences in reward processing

are more nuanced than predicted by theories that posit either global reward-related hypo- (e.g., Spear, 2000) or hypersensitivity (e.g., Ernst and Hardin, 2009; Somerville et al., 2010). Instead, these developmental differences appear dynamic, varying as a function of task features, particularly the need for decision-making. This dynamic relationship may help to explain why inconsistent results have emerged from neuroimaging studies of reward processing across development. This suggests researchers who use neuroimaging to study developmental differences in reward processing should carefully consider the precise nature of key task parameters, such as the need to make choices and the magnitude of the reward at stake. The current findings directly demonstrate the manner in which these task parameters influence neural correlates of reward processing. Moreover, the findings stimulate a re-evaluation of prior findings on developmental differences in reward processing. Findings in prior studies that appear, at first glance, to reflect global, development-related differences in reward processing, may actually reflect particular effects in one or another age group due to specific features of one or another reward task.

Specific task features are likely to differentially engage top-down cognitive processes in adolescents and adults, which in turn modulate developmental differences in sensitivity to incentive value. Behavioral data (subjective ratings of cues) collected after scanning in the current study also reveal signs of age-related differences in incentive value. Adults, but not adolescents, rated cues for large incentives obtained without decision-making more positively than cues for small incentives. However, neither adults nor adolescents rated cues for small and large incentives obtained with decision-making differently. This further suggests the capacity for task features to modulate developmental differences in reward-related processes.

While this relatively simple decision-making task engaged brain regions associated with top-down cognitive control, during scanning, no age differences in behavioral performance (RT) emerged. Therefore, the observed age-related differences in brain function cannot be attributed to age-related differences in behavior, thereby removing so-called "performance confounds" that complicate many between-group comparisons in brain imaging. Moreover, the presence of comparable task-related variation in behavior among adolescents and adults demonstrates that the current task is developmentally appropriate for adolescents.

As hypothesized, we found that neural activity among adults and adolescents varies depending on whether rewards are obtained with or without decision-making. Particularly notable findings emerge in the insula extending into putamen and components of the prefrontal cortex, including dACC, and mid-cingulate cortex. During the anticipation of rewards obtained either with or without decision-making, adults exhibit similar levels of neural activation in these regions for small and large incentives. Among adolescents, however, neural activity in these brain regions varies during reward anticipation as a function of decision-making requirements. These adolescent-limited, task-related variations reflect enhanced responding specifically for non-decision events, relative to decision events, when adolescents anticipate large, compared with small, incentives. These findings suggest that both reward magnitude and task-related decision-making requirements differentially influence the adolescent and adult brain. Moreover, prior research finds that activity in the striatum, anterior insular cortex, dACC and mid-cingulate cortex varies with changes in stimulus salience (Habas et al., 2009; Seeley et al., 2007; Sridharan et al., 2008). Considered in light of the current findings, this suggests that adolescents may therefore be more likely to engage bottom-up saliency-driven, rather than top-down goal-driven, processes as they consider large relative to small incentives under conditions that do not require explicit decision-making.

Whereas prior reward-based studies report developmental differences in striatal and prefrontal function, here we also found distinct results in the precuneus during receipt of rewards that were obtained without decision-making. While adolescents exhibit similar levels of neural activation in this region, regardless of incentive size, adults are more responsive to large, compared with small, rewards. This age-related finding is interesting in view of the involvement of the parietal cortex in reward-related behavior (Ernst and Paulus, 2005), particularly in decision-making of uncertain outcomes (Funahashi, 2001; Reyna and Farley, 2006; Steinberg, 2007). However, this was only a medium size-effect, and clearly requires replication. Nevertheless, as with reward anticipation, this finding highlights the nuanced nature of developmental differences in reward receipt. If replicated, such findings would further suggest that adults and adolescents engage distinct cognitive and associated neural processes based on reward-processing stages, decision-making requirements, and incentive size.

As hypothesized, when rewards are obtained with cues that explicitly engage decision-making, developmental differences in neural response to incentive size are eliminated. By directly contrasting events with and without decision-making, these findings show that, while adolescents have the capacity to engage similar brain regions as adults, they may not do so unless top-down cognitive processes are activated by situation-based demands, such as the need for decision-making. In other situations that require reward-processing, adolescents may be more likely than adults to rely on saliency-driven, bottom-up mechanisms (e.g., Ernst and Fudge, 2009; Smith et al., 2011; Steinberg, 2007). Given these data, it is not surprising that prior neuroimaging findings in developmental reward processing appear inconsistent. For example, tasks that do not require decision-making often result in developmental differences in striatal activity during reward anticipation, but not receipt (Bjork et al., 2004, 2010; Geier et al., 2010), whereas tasks with decision-making often find the opposite results (Ernst et al., 2005; Eshel et al., 2007; van Leijenhorst et al., 2010a). Further inconsistencies may relate to the failure to isolate neural response to large and small rewards (Eshel et al., 2007) as well as processes occurring during reward anticipation vs. receipt (Galvan et al., 2006; Smith et al., 2011).

4.1. General implications and limitations

The current study has important implications for brain-imaging research on age-related variation in reward processing. This study identified two parameters, decision-making and incentive size, that differentially influence developmental differences in reward processing. There may be other task-related parameters that have similar or even more pronounced effects on outcomes. Such findings challenge theories of global hypo- and hyper-reactivity to reward among adolescents. Rather, situational factors, such as the magnitude of a reward or the need to make a choice, play an important role in modulating developmental differences in response to reward.

The current study also bears some broader implications. Adolescent and adult sensitivity to incentive value varies based on whether rewards are obtained with or without decision-making. Understanding normative brain mechanisms such as these is critical for deciphering atypical processes in patient populations. For instance, decision-making differentially modulates reward function in typically developing vs. behaviorally inhibited adolescents (Bar-Haim et al., 2009; Helfinstein et al., 2011); the latter are at risk of developing anxiety disorders (Chronis-Tuscano et al., 2009). Studies show differences between these populations in neural response during reward anticipation (Bar-Haim et al., 2009; Guyer et al., 2006) and receipt (Helfinstein et al., 2011). Most studies only contrast brain activity in healthy and at-risk or patient populations during one form of reward processing. This is because adequately powered tasks contrasting activity across multiple forms of reward processing must include multiple factors, forcing implementation of long tasks. Yet, psychological deficits intrinsic to anxiety and depression may be particularly sensitive to cognitive factors, such as decision-making, that modulate incentive processing. Identifying these factors may help isolate cognitive strategies that could be used to reset otherwise dysregulated reward processing.

The study has limitations. For instance, the wide age range of subjects may introduce noise. Thus, more caution is needed for negative than positive findings. Despite this limitation, at least some of the expected between-group differences emerged. Future research should recruit homogeneous age groups, which would also permit the study of puberty effects and other factors operating within adolescence.

The current findings can only hint at the precise nature of real-world contexts that elicit greater risk-taking in adolescents than adults. This is because real-world contexts often differ quite markedly from the contexts of neuroscience experiments, where methodological concerns require the use of precise restrictions on task design. Thus, unlike in experimental contexts, where top-down and bottom-up processes can be manipulated and isolated from one another, real-world contexts typically involve complex blends of these two sets of processes. Thus, considered against the complex backdrop of real-world scenarios, the current findings suggest that it is not the mere requirement to engage either top-down or bottom-up processes that lead adolescents to behave differently in particular contexts, but rather the relative combination of these two processes in different contexts. Specifically, reward-driven behaviors among adolescents are expected to manifest uniquely in contexts where bottom-up, stimulus-driven aspects of the context heavily influence behavior, even though such behavior reflects the mutual influence of bottom-up and stimulus-driven influences.

In real-world contexts, the propensity of adolescents to engage in risky, but rewarding situations, such as drug use, driving too fast, or unsafe sex, may be modulated by decision-making. The current findings suggest that such adolescent-specific behavioral tendencies manifest in contexts heavily shaped by stimulus-driven features, presumably due to age-differences in stimulus-driven engagement of the reward circuitry delineated in the current study. A better understanding of how context and its associated stimulus-driven processing influence adolescent behavior in such situations could have important implications for the formulation of interventions aimed at preventing risk-taking behavior.

Probably the best-studied example of adolescent-specific stimulus-driven behavior focuses on risk-taking while driving. Adolescents face higher risk for traffic accidents than adults (Cvijanovich et al., 2001), and such accidents are more likely to occur among adolescents who are driving with peers, relative to those who are driving alone (Chen et al., 2000). Work by Steinberg and colleagues suggests that the presence of peers more heavily influences risk-taking behavior among adolescents than adults (Steinberg, 2004, 2007, 2008). Considered in light of the current work, peers can be viewed as a highly salient stimulus feature of a potentially risky environment, one that shapes the context of driving by imbuing it with highly rewarding stimuli. Thus, unlike driving alone, where behavior can be heavily shaped by top-down, rather than bottom-up processes, driving with peers imbues a situation with salient, distracting, bottom-up, stimulus features. The presence of peers can "tip the balance" towards stimulus-driven, bottom-up processes and away from top-down processes. This contextual feature, in turn, might lead to the age-related differences in behavior that presumably relate to neural correlates of the stimulus-driven differences found in the current work. Taken together, this current and prior work should encourage researchers to find other instances where stimulus-driven aspects of a context lead to age-related differences in real-world behaviors.

An additional limitation is that probability of reward receipt co-varied with decision-making, such that 100% of no-choice trials but only 50% of choice trials led to rewards. This difference in outcome probability has important implications for the cognitive processes engaged during reward anticipation. Indeed, no-choice cues signal both the absence of decision-making and certain reward receipt, while choice cues signal both the need for decision-making and uncertain reward receipt. Thus, differences in neural response between choice and no-choice cue-conditions may reflect differences in decision-making and/or the certainty of the reward outcome. Moreover, the reduced likelihood of a reward decreases the value of that reward, which is captured by the computation of expected values as the product of probability by magnitude of the reward

(e.g., Tversky and Kahneman, 1992). As a result, differences in outcome probability might cause reward magnitude to become more salient for adolescents. Interpreted in this way, increased activity in regions such as the cingulate cortex and anterior insula may reflect that reward magnitude is more salient for adolescents than adults, but only when those rewards are certain to be obtained. This potential confound is clearly a serious limitation in the current design, and is critical to clarify in future work. However, this issue underscores the need for researchers studying developmental differences in the neural substrates of reward processing to consider carefully how small alterations in experimental parameters can result in different findings.

Finally, a relatively high rate of motion-related attrition occurred among adolescents in the current study. There are several factors that may have contributed to motion artifacts. The adolescents with excessive motion artifacts tended to be younger than those without excessive motion. Younger adolescents may have had a more difficult time with a long task (~25 min), which required them to attend and perform adequately over this relatively extended period of time. While these task features have the advantage of maximizing statistical power and generating important behavioral data, they may contribute to a relatively high rate of data loss due to poor task compliance or excessive movement. However, the pattern of excessive motion was not homogeneous across all subjects. While some subjects exhibited more pronounced motion during the final run of the experiment, in others motion was more prominent near the end of each run or throughout the entire task. This suggests that the relatively long duration of the task may have contributed to the excessive motion exhibited by some adolescents, while fatigue within each run may have been more problematic for others. Adolescents who exhibited motion throughout the task may have benefitted from formal motion-limitation training in a mock scanner prior to the experiment. Despite the relatively high rate of attrition that we observed, the vast majority of adolescents were able to successfully complete the task without excessive motion.

In summary, the current findings demonstrate that decision-making differentially influences neural sensitivity to incentives in adults and adolescents. The modulatory effects of decision-making may contribute to risk-taking proclivity in adolescence and risk for psychopathology. Follow-up research is warranted to confirm the present findings and delineate the mechanisms underlying these effects.

Conflicts of interest

The authors have no conflicts of interest.

Acknowledgments

This work was supported by the Intramural Research Program of the National Institute of Health, National Institute of Mental Health. The authors would like to thank Nancy Adleman, Jennifer Britton, and Rick Reynolds for their invaluable advice on data analysis.

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.2012.04.002.

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