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Developmental Trends and Individual Differences in Brain Systems Involved in Intertemporal Choice During Adolescence

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This study used functional magnetic resonance imaging (fMRI) to examine the neural systems activated during an intertemporal choice task in a group of 14- to 19-year-old adolescents, as well as the relationship of such activation patterns to individual differences in the self-reported ability to engage in nonimmediate thinking (i.e., less impulsive and more future-oriented thoughts and action). With increasing age, there was greater differentiation between patterns of brain activity for immediate versus future choices across three distinct brain systems involved in intertemporal choice—those involved in exerting control over behavior, attributing affective value to choices, and imagining future outcomes. Furthermore, a greater propensity toward self-reported nonimmediate thinking was associated with decreased activity in the systems involved in cognitive control, possibly suggesting that individuals with greater self-reported nonimmediate thinking need to rely less on cognitive control regions during conditions of intertemporal choice. These results highlight the role that both developmental age and individual differences play in influencing neural systems involved in intertemporal choice. Implications for understanding the onset of substance abuse disorders during adolescence are discussed.

Keywords: adolescence, intertemporal choice, planning, fMRI, brain systems, impulsivity

The focus of the current study was to examine the activation of neural systems during adolescence that underlie intertemporal choice. Tasks involving intertemporal choice are those in which an individual makes a series of decisions between an immediately available reward, and a larger, but temporally delayed, reward. For example, an individual may be given a hypothetical choice between receiving $300 now or receiving $600 in 3 months time.

Generally, in such intertemporal choice tasks, the future reward must be greater in objective value than the immediately available reward for it to be chosen. The term "delay discounting" reflects the fact that people discount the value of a future reward compared with an immediate reward. Furthermore, the longer an individual must wait for the delayed reward, the larger it must be to seem attractive compared with an immediate one (Berns, Laibson, & Loewenstein, 2007; Frederick, Loewenstein, & O'Donoghue, 2002). In essence, a bird in the hand today is worth more to people than two birds in the hand at some point in the future.

A number of factors influence the ability to delay reward. Traditionally, trait impulsivity was thought to be a major factor that influenced the degree to which an individual is likely to choose a delayed reward. Increased self-reported impulsivity as determined by a questionnaire (i.e., the Barratt Impulsiveness Scale—BIS10R) that measures the ability to act without thinking (motor impulsivity), to make decisions on the spur of the moment (cognitive impulsivity), and to fail to plan ahead (nonplanning impulsivity) has been found to be associated with a decreased ability to delay reward (de Wit, Flory, Acheson, McCloskey, & Manuck, 2007). Difficulty in choosing delayed rewards and a preference for immediate rewards is characteristic of certain populations, such as individuals who abuse substances (for review, see Kirby & Petry, 2004; Reynolds, 2006; Rossow, 2008). From these findings and others, it has been suggested that an inability to delay a reward is both a contributor to and a consequence of drug use (see de Wit, 2009, for review).

However, more recently researchers have suggested that individual differences in cognitive factors, such as the ability to imagine and experience pleasure or pain in advance of a future event, or the manner in which the choice itself is framed, may also influence intertemporal choice (e.g., Berns et al., 2007). The importance of future orientation, the overarching ability to imagine and plan for the future, was recently demonstrated in a delay-discounting study of over 900 individuals, ranging from 10 to 30 years of age (Steinberg, O'Brien, Cauffman, Graham, Wollard, & Banich, 2009). The results indicated that the ability to delay reward increases with age, with a notable increase occurring around age 16. Concomitant with this change were age-related decreases in self-reported impulsivity as assessed by subscales of

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the Barratt Impulsiveness Scale (Version 11) examining motor impulsivity, inability to delay gratification, and lack of perseverance (Steinberg, Albert, Cauffman, Banich, Graham, & Woolard, 2008) along with age-related increases in self-reported future orientation, as assessed with regards to the ability to take a time perspective (i.e., think about the future), to anticipate future consequences, and to plan ahead. However, at least in this developmental time frame, self-reported future orientation was a better predictor of the ability to delay rewards, even when taking self-reported impulsivity into account (Steinberg et al., 2009), highlighting the degree to which nonaffective factors may influence the ability to delay reward.

Neural Mechanisms of Intertemporal Choice

In a recent review, Peters and Büchel (2011) propose a model in which three distinct brain systems influence individual differences when making intertemporal choices. According to their model, one system supports the representation of the subjective value of the options, another supports self-control, conflict resolution and strategy adaptation, and a third provides the ability to imagine or represent the future. Because we find this framework particularly rich, we utilize it to consider changes in the neural systems supporting decisions involving intertemporal choice during adolescence. Below we briefly discuss each of these systems, as well as evidence that they are undergoing important developmental changes during adolescence.

Valuation

One of the neural systems involved in intertemporal choice computes the subjective value of potential rewards to an individual; that is, the value based on personal preferences and contextual experiences, rather than based on some objective measure such as specific monetary value. The mesolimbic dopamine system, including the ventral tegmental area (VTA), ventral striatum (VS), along with the ventromedial prefrontal cortex (vmPFC) have been implicated in this process (reviewed in Ballard & Knutson, 2009; Kable & Glimcher, 2007; Rangel, Camerer & Montague, 2008; Rangel & Hare, 2010).

Of note, there is increasing evidence of both behavioral and neural changes in this valuation system during adolescence (see Casey, Jones, & Hare, 2008, for review). Behaviorally, there are changes under conditions of risky decision making (Crone & van der Molen, 2004) that appear to follow an inverted U-shaped function with maximal sensitivity to reward at midadolescence (Cauffman, Shulman, Steinberg, Claus, Banich, et al., 2010). Concomitant changes are observed in neural systems that process rewards with increased activity in the dopaminergic system, most notably in the ventral striatum, both when anticipating rewards (e.g., Galván, Hare, Parra, Penn, Voss, et al., 2006) and when receiving them (Ernst et al., 2005; van Leijenhorst et al., 2010). As a result, we might expect that intertemporal choice behavior in adolescence will be influenced by changes in neural systems supporting valuation.

Cognitive Control

Brain regions involved in cognitive control, most notably dorsolateral prefrontal cortex (DLPFC), are thought to exert a top-down bias in decision-making tasks by incorporating higher-level goals that are not represented by the valuation system (Peters & Büchel, 2011). Support for this idea comes from neuroimaging studies (Berns et al., 2007; Hare, Camerer, & Rangel, 2009; McClure, Laibson, Loewenstein, & Cohen, 2004) and studies in which brain activity is modulated directly, as by repetitive transcranial magnetic stimulation (rTMS; Figner et al., 2010) or continuous theta burst stimulation (cTBS; Cho et al., 2010). Such top-down biasing by the DLPFC may be especially important under certain conditions. For example, when two options are perceived similarly by the valuation system, additional top-down biasing may be required to select between those two choices (Figner et al., 2010). In other cases, the DLPFC is engaged when the value of rewards are known to be good but are difficult to choose, such as temporally distant offers or healthy but tasteless foods (Hare, Malmaud, & Rangel, 2011).

The neural mechanisms supporting cognitive control are undergoing important changes during adolescence (for review, see Crone, 2009; e.g., Adleman et al., 2002; Rubia et al., 2006). Moreover, such activation has been linked to self-reported control on real-world measures of cognitive and social control (e.g., resistance to peer pressure; Andrews-Hanna et al., 2011). As such, developmental changes during adolescence in cognitive control regions are also likely to play a role in tasks involving intertemporal choice.

Future Thought and Orientation

The third system highlighted by Peters and Büchel (2011) is one involved in imagining the future or future outcomes. This imagery/prospection system relies predominantly on structures within the medial temporal lobe, and regions to which they are anatomically connected, including the retrosplenial cortex, posterior cingulate cortex, lateral parietal cortex, and the vmPFC (e.g., reviewed in Andrews-Hanna, 2012; Schacter, Addis & Buckner, 2008; Spreng, Mar, & Kim, 2009). These cortical regions are also reliably recruited when individuals remember their past (Spreng et al., 2009; Svoboda, McKinnon, & Levine, 2006), suggesting that episodic memory retrieval is an important precursor to prospective thought (Schacter et al., 2008). Prospective processes may be important for intertemporal choice because they allow people to forecast and value events that are not currently affecting them but may come into play at a later time (Benoit, Gilbert, & Burgess, 2011; Cheung & Cardinal, 2005; Gilbert & Wilson, 2007; Peters & Büchel, 2010; Suddendorf, Addis, & Corballis, 2009).

With regards to adolescent development, there is a relative paucity of literature examining changes in the imagery/prospection system during this time period. However, there is reason to think that development of this system may be continuing into adolescence, because a recent behavioral study suggests that self-reported future orientation predicts delay discounting in adolescents better than self-reported impulsivity (Steinberg et al., 2009).

Neurodevelopmental Studies of Delay Discounting

To our knowledge, there is only one study to date that has examined the neural systems involved in intertemporal choice in typically developing adolescents. Christakou, Brammer, and Rubia (2011) gave a standard delay-discounting task in which choices

were adjusted based on prior answers to 40 males ranging in age from 12 to 32. They found that adolescents (under the age of 18, $N = 19$) discounted future rewards more than adults (18 or above, $N = 21$). Across both the immediate and delayed responses, Christakou and colleagues observed linear effects of age on activation in a number of cognitive control regions spanning prefrontal and parietal cortex, along with decreases in limbic corticostriatal areas. Left vmPFC was the only area in which age-related changes were also associated with individual differences in how rewards were valued. In addition, with increasing age, there was increased connectivity between control regions and the vmPFC, and between the vmPFC and ventral striatum. Hence, this study suggests that the effects of the control system increase with age, those of value system decrease, and that the corticolimbic circuitry becomes more integrated to influence intertemporal choice.

Rationale and Design

Our study was designed to expand upon prior work in a variety of ways. First, compared with the study by Christakou et al. (2011), the present study focused on neural systems underlying intertemporal choice in a more tightly focused age range, individuals between 14 and 19, because behavioral work suggests this is a critical time period for developmental changes in behavior regarding intertemporal choice (Steinberg et al., 2009). Second, it examined the developmental trajectories of the neural systems involved in intertemporal choice—cognitive control, valuation, prospection/imagery. Given that behavioral evidence suggests that both cognitive control and valuation affect intertemporal choice in this age range (Steinberg et al., 2009), we expected to see age-related changes in the brain regions related to these processes. If observed, it would provide confirmatory evidence that the processes influencing intertemporal choice during adolescence are multifaceted. Because the role of prospection/imagery in intertemporal choice in this age range is less clear, our examination of activity in related neural systems was more exploratory.

In addition, we examined how individual differences in factors unrelated to age influence patterns of brain activation. More specifically, the study explored how individual differences in a self-reported composite measure of nonimmediate thinking (NIT), which incorporated both self-reported future orientation and self-reported impulsivity, was related to patterns of brain activation. We predicted that patterns of neural activation would be influenced by individual differences in NIT.

Method

Participants

Advertisements for study participation were placed in a variety of locations throughout metropolitan Denver, including local newspapers, e-mail lists, community colleges, grocery stores, churches, local bus routes, afterschool programs, and bulletin boards at hospitals. Participants were right-handed, spoke English as a native language, and had no history of psychiatric or neurological disorders, substance abuse, head trauma, or claustrophobia. All participants of age provide informed consent, whereas the legal guardians or parents of all participants below the age of 18 provided consent on their behalf. In addition, all minors signed an additional "assent" form explaining the procedures of the study. All procedures were approved by the Colorado Multiple Institutional Review Board and participants were compensated monetarily.

Though the wider sample included participants aged 14–25 years, the present study focused primarily on individuals within the adolescent time period: aged 14–19 years. A total of 37 adolescents met the above criteria and participated in the study. However, six either failed to complete the study or produced unusable imaging data due to scanner artifacts and/or excessive movement (>2 mm linear displacement) and were excluded from analyses. In addition, two participants were excluded based on restricted behavioral performance (i.e., insufficient number of trials in critical conditions). No participants were considered outliers on overall response time (reaction time [RT]).

After eliminating participants based on the above criteria, 29 adolescents yielded usable imaging and behavioral data and their data were included in the analyses described in the present report. In addition to using age as a covariate, we also divided the group in half and compared the older half of the sample (aged 17–19; $N = 14$) to the younger half (aged 14–16; $N = 15$). Demographic characteristics of these two age groups are provided in Table 1. Independent-samples t tests indicated that the two age groups did not differ on any demographic characteristics other than age ($t = 8.38$, $df = 25$, $p < .0001$, $d = 1.35$).

Materials

Self-Report Questionnaires. Outside of the magnetic resonance imaging (MRI) scanner in a quiet testing room, participants completed a variety of self-report questionnaires. These questionnaires asked participants to rate certain cognitive, social, and emotional characteristics to assess real-world behaviors. Only the questionnaires of interest for this report are described and discussed.

To assess the degree to which participants reported engaging in future-oriented thought throughout daily life, we administered the Future Orientation Questionnaire (Steinberg et al., 2009), a 15-item questionnaire comprised of three separate subscales: Planning Ahead, Anticipation of Future Consequences, and Time Perspec-

Table 1
Participant Demographics and Descriptive Statistics of Behavioral Measures for the Older and Younger Adolescents Groups

	Younger	Older
N	15	14
Mean age	14.93	17.29**
Age range	14–15	17–19
% Males	0.47	0.5
IQ	98	104
Mother's education	12.64 years	13.21 years
Father's education	13.00 years	13.38 years
Proportion of choices (Later–Now/Total)	.15	.48*
Nonimmediate thinking (NIT)	−0.25	0.27
(Now reaction time [RT]–Later RT)/Later RT (ms)	.04	.17*

Note. group differences at * $p < .05$ and ** $p < .001$.

tive. For each item within the questionnaire, participants chose which of two opposing statements (separated by the word "BUT") best fit their own personality. Examples of statements for each subscale are listed below.

Planning ahead subscale. "Some people think that planning things out in advance takes all the fun out of things" BUT "Other people think that things work out better if they are planned out in advance."

Anticipation of future consequences subscale. "Some people have trouble imagining how things might play out over time" BUT "Other people are usually pretty good at seeing in advance how one thing can lead to another."

Time perspective subscale. "Some people would rather be happy today than take their chances on what the future may bring" BUT "Other people will give up their happiness now so that they can get what they want in the future."

Once participants selected which of the two statements best characterized their behavior, they then rated *how* characteristic this statement was of them by selecting either "very true" or "sort of true." The questionnaire was scored in accordance with Steinberg et al., 2009, by coding each set of statements using a 4-point scale, ranging from "*really true*" for the statement indicating low future orientation (i.e., response of 1), to "*somewhat true*" for that statement (i.e., response of 2), to "*somewhat true*" for the statement indicating high future orientation (i.e., response of 3), to "*really true*" for this statement (i.e., response of 4). Relevant responses were reversed-scored and averaged across items such that higher scores indicate greater future orientation.

To assess impulse control, participants completed a 15-item version of the Weinberger Adjustment Inventory (WAI; Weinberger & Schwartz, 1990), consisting of two subscales: the degree to which participants report being able to control their impulses (8 items) and the degree to which they can suppress aggressive behavior (7 items). In this measure, participants rate the self-descriptiveness of several statements such as "I do things without giving them enough thought" using a 1– 5 Likert scale (1 = *false*, 2 = *somewhat false*, 3 = *not sure*, 4 = *somewhat true*, 5 = *true*), with some items being reverse scored. Because aggressive behavior was not highly relevant for the purposes of the present study, only the score from the Impulse Control subscale was utilized. The value for this measure was then reversed to match the direction of the Future Orientation questionnaire, so that higher scores indicate better Impulse Control. The rationale for using this subscale rather than the Barratt Impulsiveness Scale was that research by our colleagues indicates that this impulsivity subscale has good psychometric properties for individuals in the age-range examined (Monahan, Steinberg, Cuaffman, & Mulvey, 2009, p. 1658).

Unlike our prior behavioral study on a larger sample ($N > 900$) in which future orientation and impulse control appeared to be assessing somewhat independent constructs, in the current sample they were highly correlated ($R^2 = .62$). This difference may be because of the smaller sample size in the present study or because in the prior behavioral study, we used a different measure of impulse control: the Barratt Impulsiveness Scale (version 11, Patton, Stanford, & Barratt, 1995). Considering the strong correlation between future orientation and impulse control in the present sample, we created a composite variable that can be conceptualized as measuring NIT. This measure was created by converting a participant's score on each scale (i.e., Future Orientation, Impulse Control Scale of the Weinberger Adjustment Inventory) individually to a z value, and then averaging across those two z values.

Assessment of IQ. To assess IQ, participants were administered a two-subtest version of the Wechsler Abbreviated Scale of Intelligence (WASI; Psychological Corporation), which has been previously normed for use by participants aged 6–89. The two-subtest version includes the Vocabulary subtest and a Matrix Reasoning subtest. Scores from the separate subtests were combined into a full-scale IQ (FSIQ) measure. Because a steeper discounting function has been associated with lower IQ (Shamosh et al., 2008), we examined the correlation of IQ with age, impulse control, and future orientation, as well as our behavioral measures of intertemporal choice. Because no significant associations were found, IQ was not included as a covariate in subsequent analyses.

Intertemporal choice task. Participants performed a variant of the delay discounting task in which the choices given to individuals were uniform across age groups rather than an iterative procedure to find each individual's indifference point. In the task, participants made binary choices between an immediate reward ("Now" option) and a reward of varying delay ("Later" option). We used hypothetical rewards, which have been shown to yield similar behavioral and neuroimaging results to actual rewards (Bickel, Pitcock, Yi, & Angtuaco, 2009; Johnson, 2002; Madden, Begotka, Raiff, & Kastern, 2003). The later option was always $1,000 dollars available at one of three future time points (1 week, 1 month, 1 year), with the value for the immediate option ranging from $190 to $960. For example, a choice might be "$1,000 in 1 month" or "$720 now." Trials were equally divided between those with a delayed reward at 1 week, 1 month, or 1 year. The range of values of the immediate option varied by age group (14–15, 16–17, 18–19) and delay (week, month, year) to be centered around the average indifference point for that delay as observed in a previous large behavioral study of differences during adolescence in delay discounting (Steinberg et al., 2009). For the 14- to 15-year-olds, the choices ranged from $190 to $960 (mean $530); for the 16- to 17-year-olds from $225 to $999 (mean $590), and for the 18- to 19-year-olds from $250 to $999 (mean $610). In particular, choices were clumped around three points: the indifference point for a given age, $200 above and $200 below. It was expected that such values were likely to lead to a 50/50 mix of Now and Later choices, a majority of Now choices and a majority of Later choices, respectively. As noted below, this approach was not successful and precluded a reliable estimate of the discounting function.

The rationale for varying the amounts shown to the different age groups, with the amount determined based on prior empirical work, was motivated by considerations that the valuation of a set theoretical amount (say $350) differs across age groups. Hence, if the amounts shown to each age group are identical, then any age differences in activation in the valuation system might occur either because we had given choices that *a priori* had different subjective values across ages and/or because of age differences in the activation of brain regions that are part of the valuation subsystem. To try to decouple these two effects, we chose to provide different age groups with choices of different values.

Individuals had 4 seconds to choose between the "Now" and "Later" reward and indicated their response on a keyboard while RT was recorded. Participants completed three runs of 60 trials each while undergoing functional neuroimaging. Trials were

pseduorandomly ordered and within each run were separated by 24 fixation trials jittered as to leave either 2 or 4 s between trials. Our analyses focused on the difference in brain activation for Now versus Later choices, examining brain activation when immediate rewards were chosen compared with delayed rewards. Of note, because of the difference in range of choices across age groups, as well as the somewhat restricted range of those choices, our procedure was not designed to focus on brain activation related either to trials with specific monetary value or on an individual's discounting function.

Procedure

Individuals performed the intertemporal choice task and answered questionnaires as part of a large multipart study that consisted of two sessions of testing on separate days. First, if over 18, informed consent was provided by the participant. If under 18, consent was obtained from the participant's parent/legal guardian and verbal and written assent was obtained from the participant. Next participants performed the intertemporal choice task described here followed by a Stroop task, the results of which are reported elsewhere (Andrews-Hanna et al., 2011). Afterward participants filled out the self-report questionnaires described below. On the second day, individuals performed another decision-making task in the magnet, after which they left the magnet and the WASI was administered.

MRI Data Acquisition. Scanning was performed on a 3T GE Signa scanner (Milwaukee, WI), with a standard quadrature head coil. Three-dimensional, high resolution, T1-weighted IR-SPGR anatomical images were acquired using the following parameters: repetition time (TR) = 9.61 ms, echo time (TE) = 3.03 ms, inversion time (TI) = 500 ms, field-of-view (FOV) = 220 mm, matrix size = 256x256, in-plane resolution = 0.86 mm × 1.7 mm, slice thickness = 0.86 mm + 1.7 mm gap, 256 coronal slices. For functional scans, we employed a fast Z-shim technique to mitigate signal dropout in areas near nasal cavities, in particular the orbitofrontal cortex and the ventral striatum—areas thought to be involved in reward processing (Du, Dalwani, Wylie, Claus & Tregellas, 2007). Twenty-nine slices were acquired using a normal EPI sequence with ramp sampling (TR = 1940 ms, TE = 32 ms, flip angle = 77, FOV = 220 mm, matrix size = 64 × 64, in- plane resolution = 3.44 mm × 3.44 mm, slice thickness = 4 mm) along with 5 additional slices for the Z-shim procedure. The 5 additional slices were localized on a participant-by-participant basis on a single EPI volume in order to maximize coverage of the artifact present in orbitofrontal cortex. The five additional z-shim slices were combined with the EPI slices covering the identical region using the formula specified in Du et al., 2007: $1.33^{*}(\text{sqrt}[\text{epi}^2 + \text{zshim}^2])$.

Stimuli were programmed using E-Prime software (Psychology Software Tools, Inc.) and were viewed through MRI-compatible goggles. Participants were given earplugs to dampen scanner noise and an air pillow was inflated around each participant's head to minimize head movement. Participants held a four-button fiber-optic button box in each hand and responded to each trial with two buttons.

Data preprocessing. To prepare the data for statistical analyses, a series of image preprocessing steps were performed using FSL tools (FMRIB, Oxford, United Kingdom, www.fmrib.ox.ac.uk). The first 7 volumes were discarded to ensure scanner intensity stabilization, followed by motion correction using a rigid-body translation and rotation algorithm (MCFLIRT) and extraction of brain tissue (BET). Next, the three functional runs were concatenated. Using FMRIB Easy Analysis Tool (FEAT), each 4D run image was spatially smoothed using an 8 mm full-width half-maximum (FWHM) Gaussian kernel, and were prewhitened with FMRIB's Improved Linear Model (FILM). The runs were joined using an intermediary higher-level analysis that averaged the estimates for the lower-level regressors using a fixed-effects model.

Statistical analyses. In the GLM, we modeled responses separately for those trials on which individuals chose the immediate option ("Now") and those in which individuals chose the later option ("Later"), treating them as separate regressors. In addition, we included a regressor for invalid responses (responses <200 ms and trials with no response). For each regressor, a double-gamma response function was convolved with an epoch of variable length, which corresponded to the RT for that trial. The variable epoch was chosen to focus on the period of the 4s trial in which the decision was being computed and to avoid modeling the remainder of the trial. A temporal derivative was included in the model for each trial in order to increase statistical fit despite variability in the peak of the hemodynamic response. FMRIB's Improved Linear Model (FILM) was used to compute the GLMs for individual participants. FMRIB's Linear Image Registration Tool (FLIRT) was used to register each participant's data to the Montreal Neurological Institute (MNI) stereotaxic template using a two-step process.

We utilized both categorical and continuous approaches to examining the effect of age. In the categorical approach, higher-level, whole-brain group analyses for each contrast of interest (e.g., Now response–Later response) were computed using FMRIB's Local Analysis of Mixed Effects (FLAME) two-stage estimate (FLAME 1 + 2), which models the within-subject variance using fixed-effects analyses and the between-subjects variances using random-effects analyses. Within FLAME, group differences (i.e., younger adolescents vs. older adolescents) for each contrast of interest were computed using two-sample *t* tests.

For the continuous approach, both with regards to age as well as other variables (e.g., NIT), higher-level whole-brain correlation analyses were performed to examine the linear relationship between brain activity and each individual's Z score (calculated across all 29 participants) on a given measure of interest (e.g., age in years) performed using FSL's robust regression to minimize the impact of outliers (Woolrich, 2008). Because an inverted U-Shaped function has been found between age and reward processing (Cauffman et al., 2010), we also ran analyses examining the quadratic relationship between brain activity and age. As these analyses yielded similar results to those with a linear effect, we do not discuss them. In addition, in some of the GLM analyses, we orthogonalized these correlations (e.g., between NIT and brain activity) with regards to another factor (e.g., age). This approach was taken to isolate those aspects of brain activity that are specifically driven by the factor of interest (e.g., NIT) independent of any shared association between that factor and the orthogonalized factor (e.g., age) with brain activity.

To determine appropriate voxel-wise and cluster-wise statistical thresholds, Monte Carlo simulations were performed using the AlphaSim algorithm (Ward, 2000). Specifically, we used AFNI's 3dFWHMx program to estimate the smoothness of the residual

images produced by FSL. Each specific contrast resulted in a slightly different smoothing kernel (ranging from 7.65 to 10.77), which we entered into AlphaSim. Our approached yielded slightly different cluster-extent thresholds for each analysis at a voxel-wise threshold of $p < .005$ (ranging from 148–170 contiguous voxels). The peak *x,y,z* coordinate in MNI space was extracted from each significant cluster and is listed in the appropriate tables, as well as the number of voxels comprising each cluster and the Z-statistic. In some cases, a significant cluster comprised a large number of voxels and spanned distinct anatomical and functional brain regions. In such cases, we list local maxima for each cluster (Table 2). Local maxima must be at least 20 mm apart and identify a new part of the cluster that is not identified by another local maxima (to avoid redundancy). This method reflects well the extent of each large cluster. The anatomical description of each significant cluster was classified primarily using the Harvard-Oxford Probabilistic Structural Atlas.

In one case (parahippocampal gyrus in Table 4), we noted a cluster that did not pass cluster correction, but was included because this region was expected a priori based on the role that memory systems play in both episodic future thought and NIT. In addition, the activation was bilateral, making it less likely that this is a spurious finding. The fact that this region did not pass cluster correction is clearly noted in Table 4 and Figure 2.

Table 2
Significant Clusters of Activation Across All Participants

Region	BA	Max Z	vox	*x*	*y*	*z*
Task > Fix						
Inferior occipital gyrus (R)	18	9.11	78,182	26	−88	−12
Inferior occipital gyrus (R)	18	9.11		26	−88	−12
Precentral gyrus (L)	6	5.84		−42	−4	42
Inferior parietal lobule (R)	40	5.24		58	−40	54
Superior frontal gyrus (R)	10	3.65		26	72	−2
Inferior frontal gyrus (L)	22	3.58		−58	10	2
Frontal pole (L)	46	3.58		−46	42	26
Medial frontal gyrus (R)	25	3.25		10	24	−20
Middle frontal gyrus (L)	8	3.24		−42	24	44
Precuneus (L)	7	3.21		−4	−68	66
Frontal pole (L)	47	3.05		−50	44	−4
Fusiform gyrus (L)	37	−6.49	12,880	−22	−42	−20
Precuneus (L)	31	−5.2		−10	−50	32
Precuneus (R)	5	−3.17		10	−42	56
Precentral gyrus (R)	4	−5.17		42	−20	46
SMA (R)	24	−3.37		12	−8	50
Superior temporal gyrus (L)	22	−3.28		−64	−4	2
Middle temporal gyrus (L)	21	−3.27		−68	−58	−6
Inferior parietal lobule (L)	40	−3.02		−58	−60	46
Insula (R)	13	−7.18	8,242	38	−16	12
Insula (R)	13	−7.18		38	−16	12
Hippocampus (R)	28	−5.29		24	−16	−20
Frontal pole (L)	10	−6.96	5,127	−10	58	−10
Middle frontal gyrus (L)	8	−4.35	200	−26	20	40
Now > Later						
Anterior cingulate (L)	32	4.65	4,147	−8	28	26
Anterior cingulate (L)	32	4.65		−8	28	26
Frontal pole (L)	10	3.87		−18	56	18
Superior frontal gyrus (L)	9	3.06		−2	54	30
Paracingulate gyrus (L)	10	2.98		4	48	−6
Inferior frontal gyrus (L)	47	4.46	3,559	−30	14	−12
Postcentral gyrus (R)	2	4.6	1,716	58	−30	50
Postcentral gyrus (R)	2	4.6		58	−30	50
Superior parietal lobule (R)	7	4.18		26	−50	56
Inferior parietal lobule (L)	40	4.36	1,072	−48	−32	40
Inferior frontal gyrus (R)	47	4.19	705	36	26	−16
Superior frontal gyrus (L)	6	3.93	526	−16	18	60
Precuneus (R)	7	3.84	458	6	−78	36
Lateral occipital cortex (R)	39	3.1		52	−68	34
Cingulate gyrus (R)	23	3.67	441	4	−22	34
Cuneus (R)	17	3.8	248	10	−84	2
Superior frontal gyrus (R)	6	4.36	228	14	8	66
Cuneus/occipital pole (L)	18	−5.36	1,564	−6	−90	8

Note. BA = Brodmann Areas; Max Z = maximum Z value in cluster; vox = cluster size in voxels, and x, y, z are peak voxel coordinates in MNI space. Whole brain search with a voxel-wise threshold of $p < .005$ and a cluster-wise alpha of .05. The specific cluster-wise threshold varied depending on the smoothness of the residual of the contrast images. Local maxima within larger clusters are cluster denoted by an asterisk (*).

Results

Behavioral Data

We first examined whether there were age differences in the proportion of Later compared to Now choices, calculated as follows for each individual: (Number of Later choices – Now choices)/(Total number of choices for that individual). Whereas Now and Later choices were chosen equally often for younger adolescents (aged 14–16, $N = 15$; mean proportion = .15; one-sample t test: $t(14) = 1.14$, $p = 0.29$, $d = 2.72$), older adolescents (aged 17–19, $N = 14$) made significantly more Later choices than Now choices (mean proportion = .48; one-sample t test: $t(13) = 5.036$, $p < .001$, $d = 1.35$), suggesting a higher propensity to chose the larger, delayed reward instead of an immediate reward. It is important to note that a statistical comparison between the two groups revealed that older adolescents chose the Later option significantly more than the younger adolescents, $t(27) = 2.07$, $p < .05$, $d = 0.77$ (Table 1). Although the bias in the older group toward a Later choice is somewhat atypical, the bias toward Later choices was greater for the Older than Younger group, consistent with less steep discounting of delayed reward in older adolescents (Steinberg et al., 2009). Despite these categorical group differences, a linear relationship with age was not observed, $r(27) = 0.21$, $r^2 = 0.04$, $p = .16$.

To examine the relative speed with which each decision was made, we examined response times for Now and Later choices by conducting a repeated-measures analysis of variance (ANOVA) on RTs specifying a within-subjects factor of Choice (Now, Later) and a between-subjects factor of Group (Younger, Older). While there was no significant main effect of Group, $F(1, 27) = .002$, $p = .96$, $\eta_p^2 = .00$, a Main Effect of Choice was observed, $F(1, 27) = 13.09$, $p < .001$, $\eta_p^2 = .33$, with responses to Later trials being significantly faster (1.61 s) than to Now trials (1.75 s). It is important to note that this effect was moderated by a significant Group by Choice interaction, $F(1, 27) = 5.76$, $p < .025$, $\eta_p^2 = .18$. This interaction occurred because whereas the Younger group did not exhibit a significant difference in RT between Now and Later choices (Now: 1.70 s, Later: 1.66 s, Paired-samples t test), $t(14) = 1.03$, $p > .32$, $d = 0.23$, the Older group was significantly faster for Later (1.60 s) than Now (1.80 s) choices; paired-samples t test: $t(13) = 3.67$, $p < .01$, $d = 1.00$. Paralleling this finding, the difference in RTs between Now and Later choices correlated significantly with age, $r(27) = 0.40$, $r^2 = 0.16$; $p < .05$.

Although RT is not necessarily a pure measure of decision difficulty because it may reflect other factors (e.g., lapses in attention; see de Wit, 2009), this pattern of findings is consistent with the idea that decisions about Now trials require more deliberation than Later trials for older adolescents. For example, increases in performance during adolescence on the Tower of London task, which requires the planning of a multistep solution, appears to be mediated by increases in the time it takes to initiate the first move (Albert & Steinberg, 2011), which likely reflects increasing deliberation before acting. Moreover, the longer the latency to first move, the lower the degree of self-reported impulsivity as measured by the Barratt Impulsiveness Scale, Version 11. Consistent with this interpretation that increased RT reflects increased deliberation, the difference in RT between Now and Later responses strongly correlated with the proportion of Later responses, $r(27) = 0.75$, $r^2 = 0.56$, $p < .0001$, even when controlling for the effect of age on both variables, $r(27) = 0.73$, $r^2 = 0.53$, $p < .0001$. In other words, individuals with a greater propensity to choose the delayed reward responded more slowly for Now choices compared with Later choices relative to those individuals with a greater propensity to choose the immediate reward. The sum of the behavioral results are consistent with the view that older adolescents are more deliberative in their decision-making compared with younger adolescence because they tended to be more biased toward the delayed response and also differentiated between immediate and delayed responses to a greater degree.

Our next question was whether such evidence of future-oriented and deliberate thought extended outside the laboratory to measures of behavior in everyday life. To do so, we investigated whether there were group differences on the composite measure NIT. This measure yielded a slight trend toward greater NIT for the older ($M = 0.27$) than younger group ($M = -0.26$), $t(27) = 1.16$, $p = .12$, $d = .56$, and no linear correlation with age (Table 1). It is interesting to note that individuals who self-reported more NIT trended toward a higher proportions of Later trials compared with Now trials, $r(26) = 0.35$, $r^2 = 0.12$, $p = .065$, and slower responses on Now trials compared to Later trials, $r(26) = 0.36$, $r^2 = 0.13$, $p = .061$, when controlling for the effect of age on both variables. This pattern of associations suggests that behavioral responding on our version of the delay-discounting task has at least some relationship to more real-world measures of underlying constructs related to intertemporal choice.

Collectively, the laboratory tasks and self-report measures converge to suggest that adolescence is an important developmental time period marked by increased tendencies toward more future-oriented and deliberate thought. However, despite these important developmental relationships, the analysis of NIT points to significant individual variability among such behaviors that cannot be solely attributed to age. The goal of the remaining analyses was to examine the neurobiological sources of this age-related and non-age related variability in intertemporal choice.

fMRI Data

Overall results. To ensure that patterns of brain activation for our version of the delay-discounting task are consistent with prior studies, we first examined the pattern of regions activated for the task in general averaged over Now and Later responses. The pattern was strikingly similar to the prior study of Christakou et al. (2011) whose population was closest in age to ours, as well as a recent meta-analysis of studies examining intertemporal choice (Carter, Meyer, & Huettel, 2010; Table 2).

Next we examined differences for the group as a whole between responses to Now and Later Choices. Results indicated a pattern typical for an intertemporal choice task with differences in activation in medial frontal cortex, fronto-polar cortex, lateral prefrontal cortex, parietal cortex, and occipital cortex (Table 2). What was somewhat atypical about the results was that such activity was greater for Now than Later trials, which likely reflects the fact that Now responses are likely to have required more deliberation and be less automatic in our task. As such, the results suggest that many of the brain regions that have previously been reported as becoming activated in intertemporal choice tasks may not be specific to a Later response, but rather are involved whenever a

difficult calculation of intertemporal choice must be made regardless of whether the ultimate choice is to select an immediate reward or a delayed one.

Relationship with age. Next we determined which brain regions showed activity that correlated with age (Table 3, lefthand portion). The contrast of Now > Later suggested increasing differentiation in the neural response to Now versus Later trials during the adolescent time period (Figure 1). Moreover, the regions that showed such differentiation span all three brain systems that have been identified as important for intertemporal choice. With regards to the control system, large regions within the prefrontal cortex showed greater activation for Now versus Later trials with increasing age, centered in the inferior frontal gyrus but extending dorsally and anteriorly to DLPFC and posteriorly to the inferior frontal junction (IFJ). With regards to the valuation system, an age-related increase was observed in the ventral tegmental area (VTA). Finally, with regards to the prospection system, increased age-related activation was observed bilaterally in the parahippocampal gyrus.

To better understand what generated these differences we examined each condition (i.e., Now, Later) versus fixation. For the contrast of Now versus fixation, increasing age was associated with increased activity in the left inferior frontal gyrus, associated with cognitive control, and the mPFC, associated with the valuation system. For the contrast of Later versus fixation, increasing age was associated with decreased activity in medial BA 8, an area involved in cognitive control. These findings suggest that increasing age is associated with increased activation of the cortical valuation system for Now choices, which may occur because these trials require more deliberation. In addition, with age there is less reliance on portions of the cognitive control system to make the Later choice, possibly because these responses are less difficult (see behavioral results).

We also examined the effect of age using a categorical approach comparing patterns of brain activation for the younger and older groups for the three different contrasts of interest (Now > Later; Now > Fixation; Later > Fixation). The patterns of effects were similar to those noted above when age was treated continuously.

Relationship with age taking behavior into account. As noted in the behavioral results, increasing age is associated with (a) an increasing proportion of Later versus Now choices and (b) an increase in RT for Now versus Later choices. On the one hand, such behavioral changes may reflect important developmental effects, which in turn, are reflected in the pattern of brain activation associated with age as described above. On the other hand, one must consider the possibility that if individuals of different ages exhibited similar behavior, no effect of age would be observed (i.e., the neural activation merely reflects the actual responses made rather than maturation of brain systems with age).

To address this concern, we conducted additional analyses to isolate those brain regions whose activation showed a significant relationship with age, when regressing out any activation associated with behavioral choice. We included in our model two covariates, more specifically the proportion increase in RT for Now

Table 3
Correlations of Brain Activity With Age in Years Image

Region	Age						Age controlling for behavior					
	BA	Max Z	Vox	X	Y	Z	BA	Max Z	Vox	X	Y	Z
Now > Later												
Cognitive control												
Inferior frontal gyrus (L)	45	4.51	3002	−56	16	8	44	4.62	2065	−58	16	18
Middle/inferior frontal gyrus (R)	45	6.14	3013	58	22	22	45	5.1	805	58	22	22
Middle frontal gyrus (L)	8	3.65	163	−28	16	52						
Superior frontal gyrus (R)	8	3.67	253	12	36	48						
Lateral frontal pole (R)							11	3.78	190	34	52	−16
Valuation												
Brain stem/VTA		4.43	648	2	−18	−16						
Prospection/imagery												
Parahippocampal gyrus (L)	30	3.89	234	−16	−44	−8						
Other												
Lateral occipital cortex (R)	39	5.47	1877	40	−74	26	39	4.55	1016	30	−78	40
Fusiform gyrus (R)	37	3.62	325	38	−64	−14	37	4.01	864	42	−64	−14
Middle temporal gyrus (R)	21	3.37	196	70	−22	−14						
Now > Fixation												
Cognitive control												
Inferior frontal gyrus (L)	44	4.66	226	−62	8	10						
Valuation												
Frontal pole/mPFC (R)	10	4.25	311	10	64	−2	10	4.13	312	22	56	−2
Later > Fixation												
Cognitive control												
Superior frontal gyrus (R)	8	−4.62	270	8	34	52						

Note. BA = Brodmann Areas; max Z = maximum Z value in cluster; vox = cluster size in voxels. *x*, *y*, and *z* are peak voxel coordinates in Montreal Neurological Institute (MNI) space. Whole brain search with a voxel-wise threshold of $p < .005$ and a cluster-wise alpha of .05. The specific cluster-wise threshold varied depending on the smoothness of the contrast. The leftside displays regions that showed a linear relationship with age. The right side shows regions that show a significant relationship with age after controlling for behavioral differences (both proportion increase in reaction time [RT] for Now vs. Later choice and proportion of Now vs. Later choices). Regions are organized in accordance with the three a priori systems involved in delay discounting—cognitive control, valuation, and prospection/imagery—or as "other" if they fall outside of these three systems.

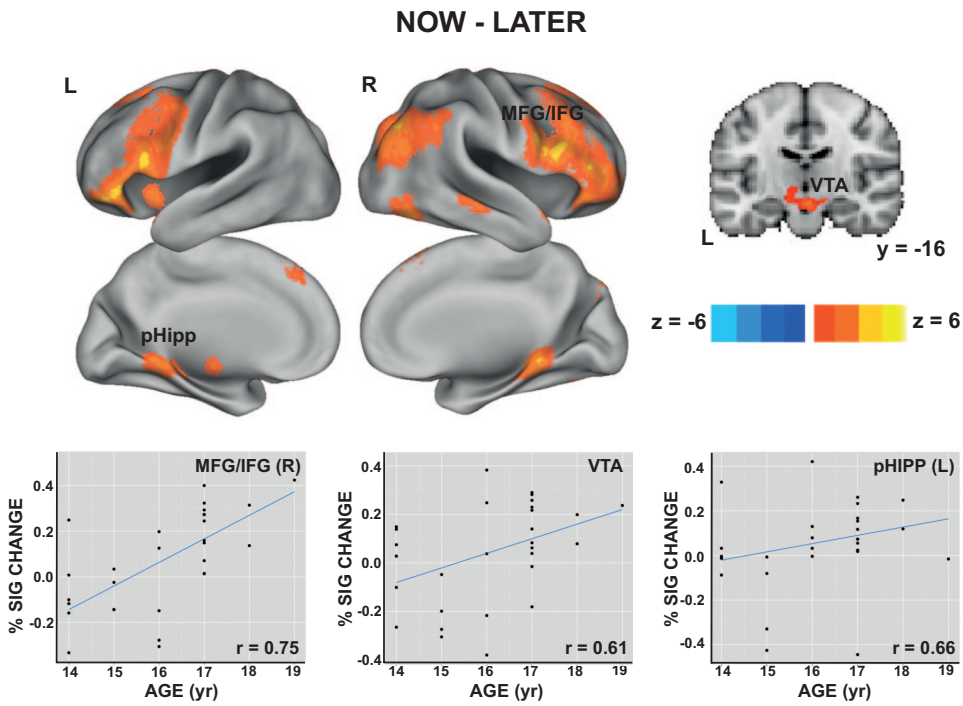

Figure 1. Age-related changes in brain activation for the contrast of Now > Later. Top, Regions that positively correlate with age for the contrast Now > Later choices are shown in warm colors. They span the control system (bilateral middle frontal gyrus [MFG] and inferior frontal gyrus [IFG]), the valuation system (ventral tegmental area [VTA]), and the imagery/prospection system (parahippocampal gyrus [pHipp]) as outlined by Peters and Buchel (2011). A voxel-wise threshold of $p < .005$ and a cluster-wise threshold of a $< .05$ as determined using Monte Carlo permutation simulations (AlphaSim) was applied to all functional magnetic resonance imaging (fMRI) images. Results are projected onto a surface template (Caret Software; Van Essen, 2005). Bottom, Scatterplots between Now > Later percent signal change and age for a representative peak region for each of the three systems (MFG/IFG: $x = 58$, $y = 22$, $z = 22$; VTA: $x = 2$, $y = -18$, $z = -16$; pHipp: $x = -16$, $y = -44$, $z = -8$) along with a regression line fitted using robust regression. For each scatterplot, fMRI activity was averaged across all voxels within a 9-mm diameter sphere centered around the peak of the cluster within that region.

versus Later choices, as well as the proportion of Now versus Later choices (Table 3; rightside; for a similar analysis examining the effect of choice on brain activation with increasing age using a different analytic approach, see Christakou et al., 2011). For the most part, these analyses yielded results suggesting that the effects observed are related specifically to age, and not to patterns of behavior or behavioral choice. This analysis yielded age-related increases in activity with age for the Now > Later contrast in lateral prefrontal cortex suggesting that the cognitive control system is specifically associated with developmental changes in brain activity. For the valuation system, effects were observed for the medial prefrontal cortex but were limited to the contrast of Now > fixation.

Also suggesting that the observed effects are because of age and not behavioral performance were the results of an additional analysis. In this analysis we selected two subgroups of adolescents (younger vs. older, $N = 12$ in each group) who were equated as to not exhibit a significant difference in either the proportion of Later versus Now choices, nor in the proportion increase in RT on Now versus Later choices (Now RT – Later RT/Later RT). Group differences were observed for all three brain systems involved in intertemporal choice, consistent with the analyses discussed above.

Relationship with NIT. We next identified those brain regions whose activity correlated with individual differences in NIT when controlling for (orthogonalizing) any association with age. Hence, the areas so identified are uniquely associated with NIT (Table 4). Increased NIT was associated with a smaller difference in activation for the contrast of Now versus Later in VI of the cerebellum (Figure 2, lefthand panel). Resting state connectivity indicate that this portion of the cerebellum is linked to DLPFC and the inferior frontal gyrus, among other regions (Bernard et al., 2012), implicating this region of the cerebellum in control-related cognitive processes. However, it remains unclear exactly what control function the cerebellum may be playing in intertemporal choice.

For the contrast of Now > Fixation, increased NIT was associated with decreased activity in portions of the cognitive control network (superior parietal regions), as well as the body of the caudate, which has been implicated in a variety of functions including reasoning (Melrose, Poulin, & Stern, 2007), executive function, emotion, sensory and motor processing (Arsalidou, Duerden & Taylor, 2012; Figure 2, middle panel). For the contrast of Later > Fixation, increased NIT was associated with decreased activity in a region of that spanned the ventral portion of the right

Table 4
Correlation of Brain Activity and Self-Report Measures of Nonimmediate Thinking (NIT) Controlling for Age Effects

Region	BA	Max Z	vox	*x*	*y*	*z*
Now > Later						
Cerebellum		−3.96	586	12	−70	−18
Now > Fixation						
Postcentral gyrus/parietal cortex (L)	40	−4.54	184	−30	−36	62
Caudate (body)		−3.85	226	−14	−12	18
Later > Fixation						
Inferior frontal gyrus/insula (R)	47	−4.66	301	44	22	−8
Parahippocampal gyrus (R)*		3.22	24	40	−22	−28
Parahippocampal gyrus (L)*		3.35	16	−26	−24	−30

Note. BA = Brodmann Areas; max Z = maximum Z value in cluster; vox = cluster size in Voxels. *x*, *y*, and *z* are peak voxel coordinates in Montreal Neurological Institute (MNI) space. Whole brain search with a voxel-wise threshold of $p < .005$ and a cluster-wise alpha of 0.05. The specific cluster-wise threshold varied depending on the smoothness of the contrast image.
* Did not pass cluster correction but was included because of bilateral activation and apriori assumptions.

inferior frontal cortex and the anterior insula, regions also involved in cognitive control (Aron, Robbins, & Poldrack, 2004; Nelson et al., 2010; Figure 2, righthand panel). In sum, these findings suggest less of a need for individuals higher in NIT to engage cognitive control regions than those lower in NIT. Although it did not pass cluster correction thresholds but was an area *a priori* of interest, we observed that increased NIT was associated with increased parahippocampal activity bilaterally (Figure 2, righthand panel). This finding raises the possibility that individuals with greater NIT employ the prospective system to a greater degree than individuals with lesser NIT.

Discussion

Relationships of Age and NIT to Control, Valuation, and Prospection Systems

The results of the current study suggest important developmental changes in all three of the neural systems posited by Peters and Büchel (2011) to play a role in intertemporal choice—control, valuation, and prospection. Perhaps the most striking finding was that activity across brain regions implicated in aiding in intertemporal choice became more differentiated for Now versus Later choices with increasing age during adolescence. As such, it suggests a developmental trajectory during adolescence in which thinking about the relative merits of rewards in the present versus those in the future may start to be treated differently. While not directly in conflict with models suggesting that cortical control regions slowly gain control over highly active reward systems during adolescence (e.g., Casey & Jones, 2010), the current findings suggest a somewhat more complicated picture. Of note, it highlights the contribution of the prospection system, which has been hypothesized to be important for projecting the future value of reward and actions. Currently, the development of this system during adolescence has been relatively unexplored, and hence seems ripe for future investigation.

Because behavior varied across age, the study also examined which of the age-related changes remained when such behavioral differences were considered statistically. Although one cannot truly control for these differences (Miller & Chapman, 2001), and indeed, they may indeed represent important developmental effects, it is nonetheless instructive to consider the pattern of results. Notably, what age differences remained after taking into account differences in behavioral performance were generally related to the cognitive control system, and mainly, but not exclusively, involved frontal regions (Table 3, righthand side). These findings highlight the ongoing development and engagement of prefrontal regions in decision making during adolescence and are consistent with our prior results indicating increased engagement of these regions during adolescence for cognitive control over nonaffective stimuli (Andrews-Hanna et al., 2011). They are also consistent with our prior behavioral work suggesting that nonaffective factors play an important role in the ability to delay reward during adolescence (Steinberg et al., 2009).

Also of importance was the finding that patterns of brain activity were related to individual differences in a composite measure of NIT (that indexed the joint variance between Impulse Control and Future Orientation) independent of age. In general, the pattern of results suggests that the more a youth engages in NIT, the less there was a need to engage cognitive control in making decisions regarding current or future rewards. Although this result may seem counterintuitive, in that one might expect those adolescents with greater rather than less NIT to have engaged cognitive control regions to a higher degree, this finding is consistent research indicating that superior performance in nonclinical groups can be associated with reduced rather than increased brain activation (e.g., Burgess et al., 2010; Sheridan, Hinshaw & D'Esposito, 2007). There were also hints of potential involvement of the prospection system, as increased NIT was associated with increased activity in the parahippocampal region bilaterally, although the level of activity for these regions did not reach significance levels required for cluster correction.

Of note, the regions isolated in the NIT analysis are nonoverlapping with those identified in the age analysis. For example, the parahippocampal region that was identified as being sensitive to age effects is more posterior and discontinuous with that identified as associated with NIT. Statistically, it is possible that activity in a given region could be influenced by both factors simultaneously,

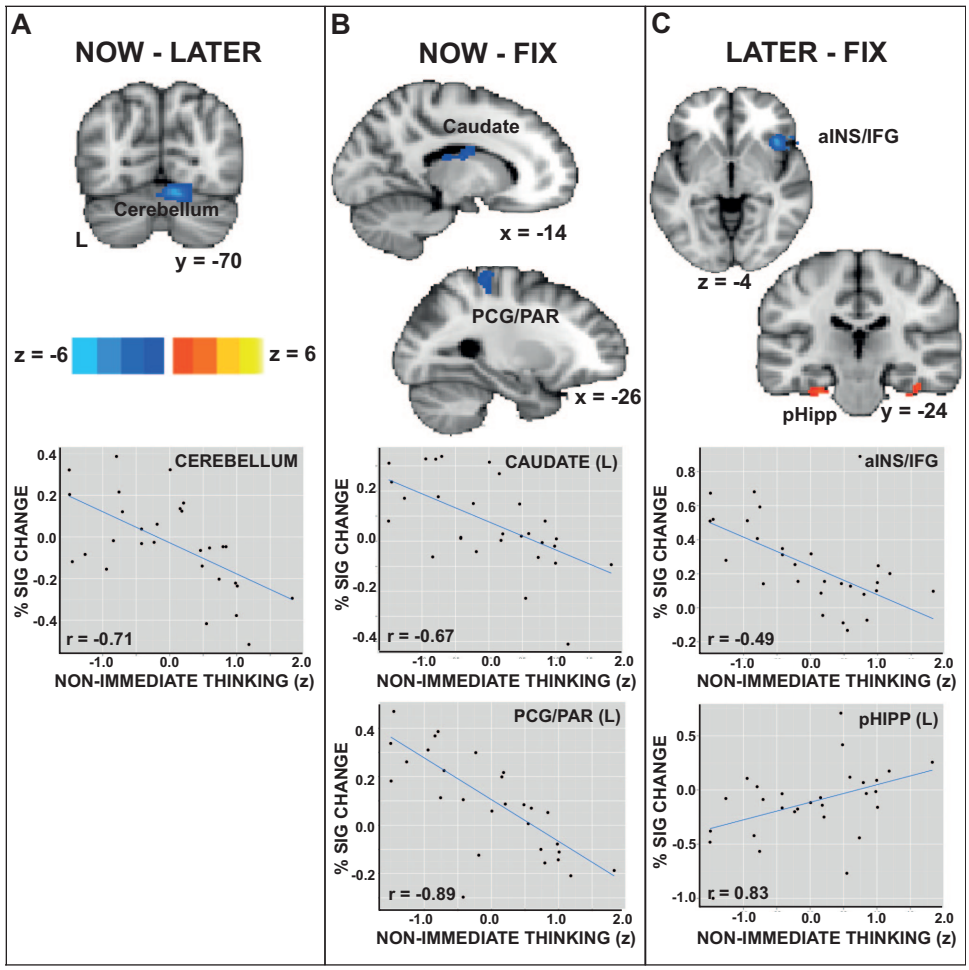

Figure 2. Brain regions whose activity are correlated with nonimmediate thinking independent of effects of age. Top, Shown in each section are the following contrasts: (A) Now > Later, (B) Now > Fixation, and (C) Later > Fixation with warm colors representing positive correlations and cool colors representing negative correlations. Regions whose activity correlates negatively include the left cerebellum, the postcentral gyrus/parietal lobule (PCG/PAR), the body of the caudate, and the right anterior insula/inferior frontal gyrus (aINS/IFG), while regions whose activity correlates positively includes portions of the parahippocampal cortex (pHipp) bilaterally. A voxel-wise threshold of $p < .005$ and a cluster-wise threshold of a $< .05$ as determined using Monte Carlo permutation simulations (AlphaSim) was applied to all fMRI images with the exception of the pHipp, which was an *a priori* region of interest and was therefore not cluster-corrected (see text). Bottom, Scatterplots of the relationship between fMRI percent signal change and nonimmediate thinking for these regions are shown below with a regression line fitted using robust regression. For each scatterplot, fMRI activity was averaged across all voxels within a 9 mm diameter sphere centered around the peak of the regions highlighted in the slices (pHipp: $x = -26$, $y = -24$, $z = -30$; PCG/PAR: $x = -30$, $y = -36$, $z = 62$; aINS/IFG: $x = 44$, $y = 22$, $z = -8$; Caudate: $x = -14$, $y = -12$, $z = 18$; Cerebellum: $x = 12$, $y = -70$, $z = -18$).

but independently. Yet in the current study the set of regions whose activity is associated with age appears to be separable from those influenced by NIT. As such, the pattern that emerges from the present study is one suggesting that a complicated interaction between developmental effects and individual differences in NIT influence delay-discounting behavior during adolescence.

The results of the current study stand somewhat in contrast to Christakou et al. (2011). In their sample of 40 males ranging in age from 12 to 32, they found that increasing age was associated with linear increases in activity in portions of the DLPFC, vmPFC, parietal and superior temporal regions along with linear decreases in activation in the ventral striatum, insula, anterior cingulate, occipital and other portions of parietal cortex. In addition, they found that with increasing age there was increased functional coactivation of vmPFC with the DLFPC for delayed reward and with the ventral striatum for immediate reward. They interpreted this pattern as suggesting that maturation of fronto-striatal circuitry is associated with increase in the ability to delay reward with age. They also found that the only region of the brain in which increasing activity with age was also associated with behavioral changes, as indexed by reduced discounting of future

rewards, was a portion of the left vmPFC during immediate reward. As such, they suggested that this region as well as its connectivity to other brain regions may play an important role in maturational and behavioral changes in delay discounting.

Our results are consistent with theirs in suggesting increased activation of prefrontal cognitive control regions with age. Although we did not find any effects of age for the ventral striatum, we did find activation in the VTA in the contrast of Now versus Later and of the anterior regions of the right vmPFC for Now versus Fixation, the latter effect which remained even after age differences in behavior were considered. Thus, our results are consistent with theirs in suggesting age-related changes in cognitive control regions as well as those related to valuation. In addition, our study additionally suggests that age-related changes in the prospection system may also influence intertemporal choice.

There are a number of potential reasons for the differences in results between their study and ours. First, their sample included a much large age range, from 12 to 40, whereas our focused on development during the narrower age period, that of 14 to 19. Second, their study was limited to males, whereas ours included both males and females. Third, we used a different method than they did to assess behaviors related to intertemporal choice. Finally, we used a stringent cluster-wise correction for consideration of statistically significant results. For example the region of vmPFC that they found sensitive to both age and behavioral effects consisted of just 8 voxels, and many of the regions that they discuss in their results consist of clusters of well under 100 voxels. Hence, differences in the criteria used to deem regional brain activation as being significant may have contributed to the dissimilarities observed between their study and ours.

Implications for Substance Abuse

A heightened bias to select an immediate compared with a delayed reward has been linked to the predisposition, acquisition, and maintenance of substance abuse. For example, a bias toward immediate rewards is predictive of individuals who are at risk for substance abuse (see Carroll, Anker, Mach, Newman, & Perry, 2010 for review), such as individuals with a family history of substance and alcohol abuse (Acheson, Vincent, Sorocco, & Lovallo, 2011). Individuals who actually abuse substances also exhibit such a bias (for reviews, see Reynolds, 2006; Yi, Mitchell, & Bickel, 2010). Moreover, a bias toward immediate reward has been recently demonstrated to predict treatment outcome for substance abuse in adolescents (Stanger et al., 2012). Hence, understanding the behavioral and neural systems underlying intertemporal choice is likely to have important implications for identifying individuals at risk for substance abuse and for those who are likely to need more intensive therapeutic interventions once they have become dependent on substances.

Our results, and those in the larger literature, suggest that tasks of intertemporal choice affect a variety of brain systems. As such, there are likely to be multiple factors that can lead to a bias toward choosing an immediate reward over a delayed one. This pattern of findings has important implications for potential treatment because it indicates that impulsive choice for a current reward might result because of (a) an inability to control or inhibit urges or prepotent responses (i.e., deficits in the cognitive control system), (b) an overvaluation of rewards (i.e., alterations in the valuation system, or (c) an inability to conceptualize the future (i.e., alternations in the prospection system).

Our results suggested that activation of cognitive control regions was related to age and also to individual differences in NIT. With regards to age, interventions to preclude the onset of substance abuse during adolescence would be well to consider the age of the targeted group. For example, at younger ages, on average the neural machinery required to "Just Say No" may not yet be mature enough to be effective. In addition to age effects, individual youth may also vary in their ability to invoke such cognitive control, as indicated by the variation in patterns of brain activity related to NIT.

With regards to valuation, we found that cortical regions (e.g., vmPFC) were affected by age but not as clearly by individual differences in NIT. These findings are consistent with the suggestion that impulsive behavior in adolescence is partly due to underdeveloped cortical valuation systems (Galván et al., 2006). In particular, it has been proposed that impulsive behavior in adolescents arises not merely from an overactive reward system in the striatum, but rather because it is coupled with an underdeveloped vmPFC. Thus, interventions that consider how adolescents value rewards versus punishments may be particularly fruitful to pursue.

Finally, the role of the prospection system in substance abuse is relatively unexplored, but may play a role in that the ability imagine the future relies, in part, on being able to access memories from the past that are relevant and related. We found age-related increases in activity in posterior portions of the parahippocampal gyrus and a hint of an influence of NIT on more anterior regions of the parahippocampus bilaterally. To the degree that younger adolescents will have fewer memories than older ones, they may have less of a storehouse of memories on which to base their predictions about the future. These findings also suggest the possibility that environmental experiences may have an important influence with regards to how choices are perceived. Consider a young adolescent experimenting with drugs for the first time. If that experience is positive—good feelings when getting high, acceptance by friends or increase in status, sense of thrill and adventure—that will be encoded by a memory system and could potentially bias valuation toward current reward. Many such experiences might build upon that initial bias and increase it. If on the other hand that initial experience is negative—altered feelings leading to anxiety or a sense of loss of control, punishment by elders or authorities, disconnection from peers—then the system may become biased toward considering future outcomes, which once again, could snowball with increasing numbers of such experiences. Such considerations provide the possibility that an adolescent's early experiences with substance of abuse may provide a memory base from which the value of using drugs can possibly be enhanced, but may also be reduced. Thus, it suggests that experiences during this developmental period may be particularly important.

Potential Limitations

The current study has certain limitations that should be noted. First, we did not use a typical delay discounting procedure that hones in on an indifference point where the subjective value of an immediate choice is equal to that of a delayed choice. As such, the generalization of our results to studies using this more traditional

method of examining delay discounting may be limited. Nonetheless, the areas activated by our version of the task overlap with those reported in a meta-analysis of tasks involving intertemporal choice (Carter et al., 2010) as well as with an empirical study by Christakou et al. (2011) in which the age of half of the participants overlapped with ours.

The method we did employ, one in which the value of immediate choices given to individuals of different age groups varied based on prior research (Steinberg et al., 2009), was intended to be sensitive to the fact that the same amount of money in a delay discounting task appears to have different value for individuals of different ages. However, we may have introduced other confounds, such as the possibility that different age groups found the task to be of varying degrees of difficulty. In addition, because of the different range of monetary choices across age groups as well as the somewhat restricted range of those choices, our procedure prohibited us from effectively calculating an individual's discounting rate with any degree of confidence.

Another potential limitation of the current study is that we did not find the typical bias toward Now choices. Nonetheless, our data did yield evidence for a developmental trend toward a greater proportion of Later choices in older adolescents, consistent with other studies in the literature finding less steep discounting functions with increasing age (Christakou et al., 2011; Steinberg et al., 2009). Moreover, our RT data are consistent with the idea that older adolescents were more thoughtful and deliberative for Now compared with Later choices than were younger adolescents. It should be noted, however, that RT is not a pure measure of difficulty, thoughtfulness or deliberation and might index other processes as well such as attentional lapses. However, if RT does index, at least in part, some aspect of difficulty or deliberation, then the more extensive activation of prefrontal regions involved in cognitive control with increasing age for the contrast of Now > Later trials would not be surprising, as these regions are known to be engaged under conditions of high demand. Our findings are consistent with TMS studies showing that the effect of TMS over DLPFC is most pronounced for difficult intertemporal choices (Figner et al., 2010). From that perspective, the pattern of results in our study is instructive. It suggests that control mechanisms are invoked whenever intertemporal choices are difficult, and their role is not necessarily restricted to conditions in which the choice for a delayed response is selected.

In addition, there may be limitations to some of the measures used. For example, in the present study we used hypothetical choices instead of realized ones. While hypothetical and realized choices have been shown to yield very similar results in adults, this issue has not been directly tested in adolescents. In addition, our measure of impulsivity was a self-report measure that, although having good psychometric properties, is limited.

Finally, in the present study we employed a cross-sectional design, which does not provide direct evidence of change that occurs with development. Furthermore, work with longitudinal investigations will be required to determine whether the patterns we observed characterize developmental trajectories over time.

Conclusions

The results of the present study support the notion that three distinct brain systems—those involved in control, valuation, and prospection—are all involved in contributing to intertemporal choices during the adolescent time period. In particular, the results suggest that the activation of these three systems becomes more differentiated with age during adolescence for immediate versus delayed rewards. In addition, individual differences in NIT also influences activation of these systems, mainly those related to cognitive control. These results suggest a complex interplay of developmental effects and individual differences influence whether an adolescent takes a reward now or waits for one later. In addition, these findings suggest that programs designed to deter the onset of drug use behaviors as well as interventions for substance abuse during adolescence would do well to consider these factors, as well as to recognize the ongoing development of the neural systems underlying them.

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