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Development of Behavioral Control and Associated vmPFC–DLPFC Connectivity Explains Children's Increased Resistance to Temptation in Intertemporal Choice

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Human civilization is based on the successful pursuit of long-term goals, requiring the ability to forego immediate pleasure for the sake of larger future rewards. This ability improves with age, but the precise cognitive and neural mechanisms underlying its development remain elusive. The developmental changes could result either from younger children valuing immediate rewards more strongly or because older children become better at controlling their impulses. By implementing 2 tasks, a choice-independent valuation task and an intertemporal choice task, both behaviorally and using fMRI in twenty 6- to 13-year old children, we show developmental improvements in behavioral control to uniquely account for age-related changes in temporal discounting. We show further that overcoming temptation during childhood occurs as a function of an age-related increase in functional coupling between value signals in the ventromedial prefrontal cortex and brain regions dedicated to behavioral control, such as left dorsolateral prefrontal cortex during choice. These findings can help to devise measures that reduce the substantial costs of impatience to society.

Keywords: behavioral control, child development, functional development of DLPFC, intertemporal choice, valuation

Introduction

Everyday decisions regularly require us to choose between options varying in their expected short- and long-term consequences. Often, rewards available in the near future are chosen over future and potentially greater rewards. Such a preference for the more immediately available is also known as temporal discounting. Particularly young children are prone to making strikingly short-sighted choices, for example, by deciding to receive rewards immediately rather than holding out briefly for a multiple of the initial amount (Thompson et al. 1997). Typically viewed as reflecting time preference, temporal discounting as revealed by an intertemporal choice can be influenced by both state and trait variables (Peters and Buchel 2011). Among these, the ability to exert top-down control when making a decision is arguably a crucial one, where, if decisions underlie control, the temptation to choose a small reward just because it is immediately available is resisted in favor of choosing a greater reward in the future.

Choosing larger delayed rewards over smaller immediately available increases during childhood (Green et al. 1994, 1999; Prencipe et al. 2011). However, the precise mechanisms underpinning this developmental change remain poorly understood. In particular, it is not known whether the developmental changes are due to age-related decreases in the valuation of rewards in the immediate or distant future, or whether improvements in behavioral control enable older children to overcome temptation. Myopic decisions have considerable consequences for personal, societal, and economic success (Mischel et al. 1988; Thaler and Benartzi 2004; Bickel and Madden 2009). Given evidence for heightened cortical plasticity at various periods during child development compared with adulthood and therefore associated opportunity for early intervention during childhood (Quartz and Sejnowski 1997; Kolb et al. 1998; Meltzoff et al. 2009), understanding the developmental mechanisms underlying intertemporal choice is of critical importance.

By means of employing 2 tasks, a valuation and a choice task, we specifically aimed to test 2 accounts of age-related differences in temporal discounting, a "pure valuation" account and a "control-integrated valuation" account. The pure valuation account suggests that with age, the "valuation" of delayed rewards changes. It has been shown that children represent immediately available options more saliently than older age groups (Crone and van der Molen 2004). It has been argued that the steeper temporal discounting in children compared with adolescents can be explained by a preference for reward immediacy (Scheres et al. 2006). Furthermore, compared with adolescents and adults, children have also been shown to display a greater neural sensitivity of orbitofrontal cortex in response to small and more imminent rewards (Galvan et al. 2006). Even though rewards almost universally lose subjective value when they are delayed, according to this hypothesis they do so less with age (Scheres et al. 2006). Recent neural accounts of intertemporal choice propose that individual differences in adults can be explained by a single underlying neural system (Kable and Glimcher 2007) dedicated to comparing the value of available reward options, encompassing regions such as ventromedial prefrontal cortex (vmPFC), the ventral striatum (VS), and posterior cingulate cortex (PCC). Thus, according to this hypothesis, the development of an increased ability to forego immediate pleasure and wait would be a function of age-related changes in explicit valuation and associated neural signals in so-called valuation regions (vmPFC, VS, and PCC).

According to the control-integrated valuation hypothesis, children improve with age in their behavioral control and can as a result better inhibit their desire to choose immediate rewards over larger but delayed rewards. An important functional role for control in the intertemporal choice is frequently advocated in the literature (Bickel and Madden 2009; Peters and Buchel 2011; van den Bos and McClure 2013). An analogous neural account of intertemporal choice suggests that, on top of a system dedicated to valuation, intervening control processes come into play, influencing the choice process in favor of larger delayed rewards by modulating brain regions involved in valuation (Figner et al. 2010; Essex et al. 2012; Crockett et al. 2013). This mechanism has been demonstrated in the

context of other types of decisions between food options varying in taste and health, where, for instance, neural signals in the vmPFC correlate with stimulus values, but during choice these value signals in the vmPFC are correlated with lateral prefrontal cortical areas, but only in those individuals capable of implementing self-control by choosing healthy foods (Hare et al. 2009, 2011; Harris et al. 2013). A recent study provides evidence for precisely such a mechanism to operate during intertemporal choice (Hare et al. 2014). The cognitive function of behavioral control has been ascribed to the lateral and particularly the dorsolateral prefrontal cortex (DLPFC; Miller and Cohen 2001; Knoch et al. 2006; Steinbeis et al. 2012). This is one of the brain regions known to take longest to mature (Sowell et al. 2001; Gogtay et al. 2004). Therefore, according the control-integrated hypothesis, age-related changes in intertemporal choice are the result of improved behavioral control mechanisms that influence valuation during choice. Specifically, as children age, an integrated value signal of vmPFC during choice should come increasingly under the influence of brain regions involved in behavioral control; a mechanism that should also be predictive of how likely it is that future option are chosen.

To address this question, we conducted a behavioral and functional imaging (fMRI) study comparing children of different ages on 2 tasks both in- and outside of the scanner: A choice-independent valuation task (VT) and an intertemporal choice task (ICT). In the VT, children were shown individual reward options varying in both magnitude (either 2, 4, 6, or 8 monetary units, henceforth MUs) and delay (either today, in 4, 6, 28, or 56 days) and asked to rate the attractiveness of each presented option (Fig. 1*A*). In the ICT, children had to choose between 2 options differing in reward magnitude and delay. The options always consisted of a small immediate reward (2, 4, or 6 MUs today) and an alternative larger delayed reward (8 Mus in 4, 6, 28, or 56 days; Fig. 1*B*). Both tasks were coupled with real incentives in that one of the highly valued options or choices was selected randomly and implemented at the end of the study. Transaction costs were kept equal across immediate and delayed options, and participants were informed that both in case of obtaining a reward today or in case of receiving it in the future, they would be given the reward at home from their parents at the specified point in time. Thus, even receiving immediate rewards in the present implied some waiting time, which differentiates our paradigm from other studies looking at behavior with rewards that can actually be consumed immediately (Mischel et al. 1989; Casey et al. 2011).

To explicitly test for the control-integrated valuation hypothesis, we measured children's response inhibition with the stop-signal reaction-time task (SSRT; Logan et al. 1997), which is sensitive to age-related changes (Bedard et al. 2002). Several researchers have commented on the potential domain-general association between different tasks measuring impulse control, in normal adults (Muraven and Baumeister 2000), psychiatric populations (Kim and Lee 2011), as well as children (Berkman et al. 2012). A range of studies demonstrates a specific link between motor control and higher level control required in the context of complex social or economic decisions (Berkman et al. 2011; Steinbeis et al. 2012; Goldenberg et al. 2013; Nash et al. 2013). Furthermore, training inhibitory control in the motor domain leads to choices, indicating increased control

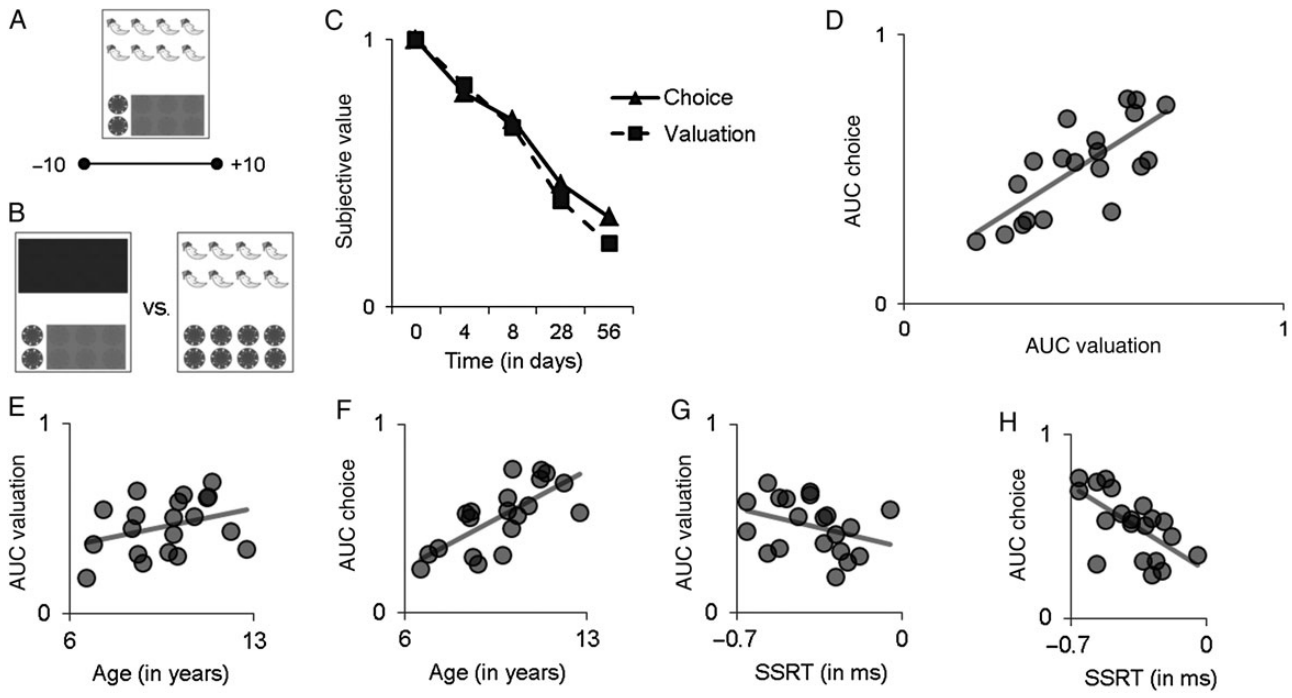

Figure 1. Behavioral data acquired during valuation and intertemporal choice. (*A*) VT design. Participants were asked to rate single options varying in terms of reward size and delay on their attractiveness (displayed here are 2 coins available in 8 days). (*B*) ICT design. Participants were asked to choose between 2 options, one delivering a small reward today (displayed here on the left 2 coins available today) and another delivering a larger reward in the future (displayed here on the right 8 coins available in 8 days). (*C*) Subjective value of rewards decreased the further they occurred in the future, both in the valuation as well as in the ICT as indicated by the averaged AUC for all subjects in each task. (*D*) Individual differences in temporal discounting in the VT correlated highly with that displayed in the ICT ($r = 0.75$; $P < 0.001$). (*E*) Whereas in the VT there was no age-related change in discounting, (*F*) in the ICT there was a significant decrease in discounting ($r = 0.718$). Equally, (*G*) while discounting in the VT did not correlate with a measure of impulse control (SSRT), (*H*) this correlation was evident in the ICT ($r = -0.633$; $P = 0.003$).

(i.e. less risky decisions) in subsequent economic decisions (Verbruggen et al. 2012) as well as restrained food consumption (Houben and Jansen 2011) and vice versa (Muraven 2010). Testing for an association between a motor-inhibition task and a task involving complex choices thus allows to test explicitly whether behavioral control plays a role in the context of intertemporal choice, which is missing from previous studies (Figner et al. 2010) especially those looking at the development of intertemporal choice.

Previous research suggests a link between general intelligence and temporal discounting (Shamosh et al. 2008), which has also been shown to improve with age (Fry and Hale 1996). We therefore used a measure of intelligence as a covariate in our analyses to ensure that such associations can be ruled out from a potential link between age, behavioral control, and intertemporal choice.

To distinguish between our 2 hypotheses, we conducted a joint behavioral and functional imaging study in children in which each participant performed both the VT and the ICT with and without simultaneous fMRI. Choices in the ICT give a direct measure of the extent to which future rewards are discounted and how this changes with age. Crucially, the separately obtained choice-independent valuation in the VT indicates the extent to which such age-related changes in choice could be due specifically to changes in pure valuation processes, while another independently obtained measure of behavioral control measures the extent to which they could be partially accounted for by control processes. These 2 accounts make several shared and unique predictions which will be outlined below. Both accounts would (1) predict a correlation between individual differences in temporal discounting in the VT and the ICT, and (2) that vmPFC tracks the subjective value of rewards.

Under the pure valuation hypothesis only would we expect there to be (3) age-related changes in the simple VT, in that the value of future rewards should increase with age. When looking at the neural activation of brain regions during the VT, we would expect (4) an age-related increase in vmPFC activity during the tracking of future values. Given that the influence of behavioral control is only argued to come into play during choice-related valuation, this hypothesis predicts (5) no correlation of individual differences in the valuation of future rewards, either behaviorally or neurally, with individual differences in an independent measure of behavioral control.

Under the control-integrated valuation hypothesis only would we expect (6) age-related changes during intertemporal choice, whereby with increasing age children will chose larger options occurring in the future more frequently and no age-related change in the valuation obtained through the VT. Given that, according to this hypothesis, we also expect (7) that behavioral control is a critical mediating factor here in bringing about this difference, we predict a correlation between individual differences in intertemporal choice and an independent measure of behavioral control. At the neural level, we expect (8) functional connectivity during choice between valuation regions such as vmPFC with DLPFC. If this control-integrated valuation mechanism is predictive of behavior, age-related changes, and linked to behavioral control, then this connectivity should increase with (9) individual differences in the intertemporal choice, whereby greater connectivity predicts a greater probability of choosing future rewards, (10) age, as well as (11) increased behavioral control measured independently using a motor control task. Of course, these hypotheses are not mutually exclusive and it is conceivable that both hypotheses are supported, in which case we would expect age-related changes during pure valuation as well as during control-integrated valuation, and see this borne out at the neural level also.

Materials and Methods

Participants

Twenty-five subjects participated in the fMRI experiment. Four had to be excluded due to excessive head movement or difficulty in understanding the task, and one due to an ADHD diagnosis. The remaining 20 subjects had a mean age of 9.7 years and a range of 6.6–12.7 years. There was an equal number of males and females in each age group. Parents of the children gave informed consent, and the study was approved by the ethics committees of the University of Zurich and of the Canton of Zurich (E96/2009). Age was treated as a continuous measure throughout all analyses.

Procedure

The study was carried out at the Laboratory for Social and Neural Systems Research. Children came in the company of their parents. There were 2 sessions for each participant. In the first session, a structural scan, a functional scan of the VT, and behavioral tests (including the ICT) were acquired. In the second session, a functional scan of the ICT and further behavioral tests (including the VT) were acquired. At most 7 days passed between the 2 scanning sessions for any of the children. Prior to the tasks in the scanner, children were shown a table stacked with rewards such as games and toys that would interest the respective age groups. The rewards were arranged from left to right by increasing attractiveness (as assessed by previous piloting). The children were told that they were going to play some games during which they could win poker chips, which they could subsequently trade in for one of the rewards. Depending on how many chips they had, the larger the range of rewards was from which they could chose (Supplementary Material).

Choice-Independent VT

Children were presented a single option displaying an amount of MUs, which were either 2, 4, 6, or 8 MUs and a point in time at which the reward would be delivered, which was either today, in 4, 8, 28, or 56 days. The amount was displayed at the bottom and the delay at the top of the screen. Each reward was presented 3 times together with each delay, producing 60 trials in total. In this task, children were asked to indicate their subjective valuation, that is, how much they liked each of the options, and were told that they would randomly receive one of the options they ranked in the top half of all possible rewards. Specifically, children were asked to explicitly rate the attractiveness of each presented option from −10 to +10 in steps of 1. To obtain a measure of response stability in the VT, ratings were obtained in both test sessions (e.g. one inside and one outside the scanner). Note that this payment scheme is incentive-compatible in that the dominant strategy is to rank the options according to their true preference ranking. To see this, suppose an individual ranked an option x1 lower than an alternative x2 (revealed preference ranking), even though option x1 was preferred to x2 (true preference ranking). In this case, if at the end of all responses x2 had the median revealed preference ranking, it would be considered in the lottery, while x1 would not be considered due to its lower revealed preference ranking, despite its higher true preference ranking. Because the set of remaining options is unknown to individuals at any point during the task, it is therefore optimal to rank any pair of options according to their true preference ranking. Maybe more convincingly, we are confident that children, when asked by an authority figure (in this case, the experimenters) to indicate their true valuations of a set of rewards of which they stand to receive one, will be highly motivated to comply with this request. Scanning occurred in 2 runs of 30 trials. An order of presentation was pseudorandomized. Each option was displayed for 10 s and followed by a cross presented between 3000 and 6000 ms.

Intertemporal Choice Task

Children were presented with 2 options each displaying an amount (either 2, 4, 6, or 8 MUs) to be delivered at a particular delay (either today, in 4, 8, 28, or 56 days). Importantly, one option always entailed a reward that could be obtained today with a value of 2, 4, or 6 MUs, whereas the alternatives had values of 8 MUs that could be obtained in either 4, 8, 28, or 56 days. Children were instructed to choose between the 2 presented options in each trial and told that one of the choices would be paid out at the end. The 3 immediately available options were each paired with each of the 4 delayed options 4 times, producing 12 trial types and 48 trials in total. This was divided over 2 runs with 24 trials each. The order of presentation was pseudorandomized. Each option was displayed for 10 s within which the child had to give a response. This was followed by a cross presented between 3000 and 6000 ms. Like the VT, the ICT was performed both in- and outside the scanner to obtain a measure of stability.

After the functional sessions, the children underwent additional behavioral testing. This included a SSRT and the colored progressive matrices (Raven et al. 2003; Supplementary Material).

To calculate the steepness of the discount function for each participant in the ICT, we obtained the indifference points from the choices between the immediate and the delayed rewards by estimating the value of the immediate reward at which subjects switch from choosing the delayed reward to choosing the smaller immediate reward. This was done using probit regression. Using the obtained indifference points in the choice task, we derived the subjective value of options presented in the future. For the VT, we used the ratings averaged over all nominal values given for each delay. We assumed there to be no loss in value for options paid out today, so ratings for each delay were normalized according to the ratings given for today and further normalized to a scale ranging from 0 to 1, with 0 indicating the lowest subjective value.

To obtain a summary measure, we used the area under the curve (AUC) to estimate the extent of temporal discounting in both tasks. This approach is agnostic to the shape of the discount curve and has been suggested as a substitute to more theoretically driven modeling approaches (Myerson et al. 2001). Specifically, we plotted the subjective values of rewards for each delay and calculated the AUC of these plots for each participant using the trapezoidal method of estimation. The AUC was normalized to [0,1]. We then used this value as the main dependent variable of the task. Smaller AUC values denote higher discounting. To test for significant associations between our behavioral variables, we used Pearson's correlations.

Imaging Data Acquisition and Processing

Brain images were acquired on a 3-T Philips Intera whole-body Scanner (Philips Medical Systems, Best, The Netherlands) at the Laboratory for Social and Neural Systems Research located at the University Hospital Zurich, equipped with an 8-channel Philips SENSitivity-Encoded (SENSE) head coil. Structural image acquisition entailed 301 T_1-weighted transversal images with a slice thickness of 1.2 mm reconstructed to 0.6 mm. For the functional imaging, a SENSE T_2*-weighted echo-planar imaging sequence was used. Thirty axial slices were acquired covering the whole brain with a slice thickness of 3 mm and an interslice gap of 0.5 mm (time repetition 1568 ms; time echo 30 ms, flip angle 90°, field of view 240 mm; matrix size 128 × 128). For the VT, a total of 316 volumes were acquired over 2 runs with 158 volumes in each run. For the ICT, a total of 456 volumes were acquired over 2 runs with 228 volumes in each run. Each run began with 5 "dummy" volumes which were discarded from further analysis.

Images were analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK) on the basis of an event-related model (Josephs et al. 1997). To correct for head movements, functional volumes were realigned to the first volume (Friston et al. 1995), spatially normalized to a standard template with a resampled voxel size of 3 × 3 × 3 mm, and smoothed using a Gaussian kernel with a full width at half maximum (FWHM) of 10 mm. Following previous studies which looked at blood-oxygenated-level-dependent (BOLD) response in children and comparing it with that of adults, we normalized all images to the same adult brain template. This approach has previously been shown to be a valid method for pediatric imaging (Burgund et al. 2002; Kang et al. 2003). A high-pass temporal filter with cut-off of 120 s was applied to remove low-frequency drifts from the data. Furthermore, subjects were excluded based on excessive head movement, which in our case entailed >1 mm in any direction.

Structural MRI Processing

FreeSurfer (Version 5.0.0; http://surfer.nmr.mgh.harvard.edu) was used to generate models of the cortical surface and to model cortical thickness from the T_1-weighted images. Previous work has validated FreeSurfer by comparing it with histological analysis (Rosas et al. 2002) and manual measurements (Kuperberg et al. 2003). Processing steps have been described in detail elsewhere (Dale et al. 1999; Fischl et al. 1999; Han et al. 2006). Following surface extraction, sulcal and gyral features across individual subjects were aligned by morphing each subject's brain to an average spherical representation (fsaverage5) that allows for accurate matching of cortical thickness measurements locations across participants, while minimizing metric distortion. The entire cortex in each subject was visually inspected and segmentation inaccuracies were manually corrected by a single rater. For whole-brain analysis, thickness data were smoothed on the tessellated surfaces using a 20-mm FWHM Gaussian kernel prior to statistical analysis. Selecting a surface-based kernel reduces measurement noise but preserves the capacity for anatomical localization, as it respects cortical topological features (Lerch and Evans 2005).

Statistical Analysis

Statistical analysis for the imaging data was carried out using a general linear model (GLM; Friston et al. 1994). Regressors were defined from the onset of the presentation of options and modeled for the duration of the rating in case of the VT, and for the duration of the individual decision in case of the ICT. In both cases, we were interested in which areas parametrically track the value of the presented options. Unlike an actual discount function (i.e. hyperbolic, exponential, and quasi-hyperbolic), which gives a subject-specific discount rate, the AUC does not provide a prediction of the subjective value of a given reward at each delay. To obtain the subjective value of each presented option during the imaging paradigm, we also calculated the subject-specific discount rate, based on the explicit valuations for the VT and the choices for the ICT. Typically, a hyperbolic decay function has been argued to provide a good estimate, which is why in both cases we used a hyperbolic model as described in the literature (Mazur 1988), where delay indicates the time of delivery (in days) and k is the individual discount parameter for each child, which indicates the steepness of the individual discount function (the larger k, the greater the discounting; see Supplementary Materials for model fits).

$$\text{Subjective value} = \frac{\text{Nominal value}}{1 + k\,\text{Delay}}.$$

For both the VT and the ICT, the correlations between the AUC and a log-transform of the subject-specific k were high (for ICT: $r = -0.881$ and for VT: $r = -0.644$).

The estimated discounted value was calculated for each delay by adding the subject-specific k and each delay to the function. After fitting the behavioral data with a hyperbolic model, we obtained a continuous regressor of the subjective value of each presented option for the imaging paradigm consisting of the subjective value of each option in the VT, and the difference in the subjective value between the delayed and the immediate option. The obtained value was then used as a regressor to see which areas parametrically track a subjective value during choice. This means that brain activity of those regions is captured which track the subjective magnitude of the delayed reward relative to the immediately available option. Even though this operationalization of subjective value has been deemed valid (Kable and Glimcher 2007), it is likely to be also predictive of the type of choice that is being made as a function of the degree of difference between the 2 options.

The regressors for the VT and ICT were convolved with a canonical hemodynamic response function. Effects of head motion were corrected for by modeling 6 motion parameters for each subject as effects of no interest in the design matrix. Subsequent contrast images were derived by applying linear weights to the parameter estimates for the regressor of each event. Contrast images were then entered into one-sample *t*-tests for random-effects analyses. Additionally, we tested for relationships between brain activity and individual differences in age, subjective valuation of rewards occurring in the future as indicated by valuation and by choice, as well as scores on the SSRT by means of entering these as covariates.

Multiple Comparison Correction

Results at the whole-brain level are reported at $P < 0.005$ (Supplementary Tables 3–9). Where applicable, correction for multiple comparisons occurred for family-wise error (FWE) using random field theory. To do so, we applied a combined voxel-height and cluster-extent correction using the AlphaSim software of the REST toolbox (Song et al. 2011). AlphSim takes into account the size of the search space (i.e. whole brain) and the estimated smoothness of the images to generate probability estimates (Monte Carlo simulations) of a random field of noise producing clusters of voxels of a given size for a set of voxels passing a given voxel-wise *P*-value threshold. The simulations yielded that a FWE-corrected threshold of $P < 0.05$ was achieved with voxels significant at a *z*-value of 2.3 in a contiguous cluster of 88 voxels.

For a priori regions involved in valuation, we corrected for multiple comparisons using small-volume FWE correction at $P < 0.05$. Volumes were constructed on the basis of the literature and thus independently of the data from the present experiment. To obtain the regions for small-volume correction of activation in value-tracking regions, we employed a two-pronged approach. In a first step, we created a mask from all activated regions tracking a subjective value during the functional run of the VT and another mask from activated regions tracking a subjective value during the functional run of the ICT. The maps from which the masks were generated were thresholded at $P < 0.01$ uncorrected. To make sure that we would only include regions typically implicated in the literature, in a second step we also created a mask derived from a recently published meta-analysis (Bartra et al. 2013), including a set of 129 studies on reward processing. These 129 studies were identified by means of a query of the subjective value database (Bartra et al. 2013) entering the following search terms: Valence: Reward; Reward Kind: Primary and Monetary; Time Period: Decision, Wait, and Reward. This yielded 2120 different foci, which were then entered into a coordinate-based analysis using the activation likelihood estimation approach (Eickhoff et al. 2009). The foci were analyzed using the GingerAle software (version 2.0.1, http://www.brainmap.org/ale/). The algorithm takes account of the sample size of each contrast and uses random-effects analysis (Eickhoff et al. 2009). The resulting map was threshholded at $P = 0.001$ (with a minimum of 200 mm^3 cluster extent), corrected for multiple comparisons by means of the false discovery rate approach (Supplementary Table 1). We then created an overlap of the interface of activated regions during the functional runs and the significant voxels from the meta-analysis. Thus, to correct for multiple comparisons in the functional run of the ICT, we took the overlap of activated voxels in the VT and the regions identified by the meta-analysis; in turn to correct for multiple comparisons in the functional run of the VT, we took the overlap of activated voxels in the ICT and the regions identified by the meta-analysis (Supplementary Table 1).

Psychophysiological Interaction Analysis

A psychophysiological interaction analysis was performed to identify brain regions showing a correlation with activity in the vmPFC during the tracking of value during the VT and ICT, respectively. Specifically we were interested in seeing if the extent of the correlation between activity of vmPFC during value-tracking and other brain regions might increase as a function of age, impulse control, and temporal discounting. Analyses were performed separately for the VT and the ICT. As a seed region from which to extract the BOLD time series, we used all significantly activated voxels at the second level in the vmPFC during value-tracking for the VT or the ICT separately at a threshold of $P < 0.005$. From this seed region derived from the second-level analysis, we extracted the mean-corrected BOLD time series for each run on the first level comprising 228 volumes from the aforementioned seed region for the ITC and 158 volumes for the VT. This BOLD time series was then deconvolved based on the model for the canonical hemodynamic response to construct a time series of neural activity in the vmPFC following procedures outlined Gitelman et al. (2003).

Subsequently, 9 regressors were entered into the GLM on the first level: The extracted time course from the vmPFC, our psychological variable of interest at each trial, which was the subjective value of each presented option as estimated using the hyperbolic function for the duration of the decision, and their interaction term as well as 6 motion regressors. In the next step, the interaction term was taken into a second-level analysis using a one-sample *t*-test. We were particularly interested in the extent to which brain regions whose activity correlated with the interaction term of the GLM would additionally vary with age and impulse control and temporal discounting. Thus, on the second level, we included age, SSRT scores, and AUC as a measure of temporal discounting and calculated separate models for each. All reported results are significant after correcting for the number of models tested for.

Mediation Analysis

To perform a mediation analysis using the extent of functional coupling between brain regions involved in valuation and regions implicated in behavioral control, we extracted the parameter estimates using a contrast image from a previous study (Steinbeis et al. 2012), in which children of the same age as in the present study had to exercise behavioral control while making a social decision and the extent to which this correlates with an independent measure of impulse control (performance on the SSRT), set at a threshold of $P < 0.05$ FWE-corrected (Supplementary Table 2). Using this contrast image, data were extracted by means of the Marsbar toolbox (Brett et al. 2002).

Results

Specific Age-Related Changes in ITC, VT, and Behavioral Control

In both tasks, subjects discounted future rewards (VT: AUC 0.461; range 0.19–0.69; ICT: AUC 0.51; range 0.23–0.76; Fig. 1*C*). There was a significant positive correlation between the AUC obtained in the 2 tasks ($r = 0.75$; $P < 0.001$; Fig. 1*D*). The first piece of evidence against the pure valuation hypothesis of age-related changes was the absence of a significant correlation between age and the AUC obtained through the valuation of single options ($r = 0.329$; $P > 0.15$; Fig. 1*E*). Equally, while the valuation of immediately available rewards (i.e. today) increased with the size of the reward ($F_{1,19} = 21.964$; $P < 0.001$), this increase did not interact with age ($F_{1,19} = 0.77$; $P = 0.524$). Furthermore, there were no age-related changes in valuation for any of the 4 reward magnitudes available today ($F < 1.6$; $P > 0.2$). In contrast, we found a significant decrease in temporal discounting with age as measured by the ICT ($r = 0.718$, $P < 0.001$; Fig. 1*F*). Importantly, this correlation remained significant after partialling out variance related to valuation ($r = 0.75$, $P < 0.001$), which suggests that age-related changes in intertemporal choice cannot be explained by individual differences in the valuation of future rewards. Furthermore, there was also a difference in slopes of the correlation between age and temporal discounting measured by intertemporal choice compared with that between age and temporal discounting measured by valuation (Hotelling Williams Test: $t = 3.89$; $P = 0.0006$). Furthermore, whereas IQ was strongly correlated with age ($r = 0.678$; $P = 0.001$) and

marginally so with temporal discounting ($r = 0.443$; $P = 0.051$), the correlation between age and temporal discounting remained significant after partialling out IQ-related variance ($r = 0.635$; $P = 0.004$). These results demonstrate that age-related changes in intertemporal choice are independent of any individual differences in the explicit valuation of rewards or age-related changes in fluid intelligence.

Further support for the control-integrated valuation hypothesis comes from additional analyses. First, temporal discounting was linked to an independent measure of behavioral control, the SSRT (Logan et al. 1997; Supplementary Material). Performance in the SSRT (where lower values imply greater behavioral control) correlated negatively with age ($r = -0.624$; $P = 0.003$) and positively with temporal discounting, that is, children with more behavioral control discounted less steeply ($r = -0.633$; $P = 0.003$; Fig. 1*H*). In addition, performance in the SSRT was unrelated to the valuation of rewards ($r = -0.334$; $P > 0.15$; Fig. 1*G*), and the correlation between SSRT and temporal discounting remained significant after partialling out variances related to explicit valuation and IQ ($r = 0.687$; $P = 0.002$). Importantly, there was a significant difference in slopes of the correlation between SSRT and temporal discounting measured by intertemporal choice, compared with the correlation between SSRT and temporal discounting measured by valuation (Hotelling Williams Test: $t = -2.052$; $P = 0.04$). This suggests a specific link between individual differences of behavioral control and intertemporal choice only. Thus, observed changes in intertemporal choice during childhood seem to be linked to age-related changes in behavioral control.

A different and complementary way of looking at specific age-related changes during intertemporal choice as a function of changes in behavioral control as opposed to valuation is by observing what happens to highly valued single options in the context of making a choice with tempting alternatives. Whereas the pure valuation hypothesis would predict that the more highly valued option should be chosen compared with the alternative, the control-integrated valuation hypothesis predicts that depending on how well behavioral control can be deployed, tempting alternatives should be yielded to. If in the context of choice temptations are yielded to, then less valued but immediately available options should be chosen, a switch that should also decrease with age (Supplementary Material). In total, the VT predicted 79.27% of the choices made in the ICT. Yielding to temptation occurred on 4.83% of choices and indeed younger children yielded to temptation more often than older children ($r = -0.392$, $P = 0.048$, one-tailed; Fig. 2). Thus, in some cases in the context of choices, younger children fail to implement what they value when faced with tempting alternatives, which further confirms the hypothesis that the development of behavioral control accounts for the age-related changes in intertemporal choice. The reverse analysis of age-related changes in choosing large late options in spite of valuing small soon options revealed an age-related increase of such switches, which was, however, driven entirely by one subject over 2 SDs from the mean, and can therefore not be interpreted.

Stability of Decision Noise

Decisions can be prone to error and noise (Gold and Shadlen 2007; Resulaj et al. 2009). To test if the age-related decrease in temporal discounting observed in the ICT is merely due to a decrease in decision errors with age, we also checked for

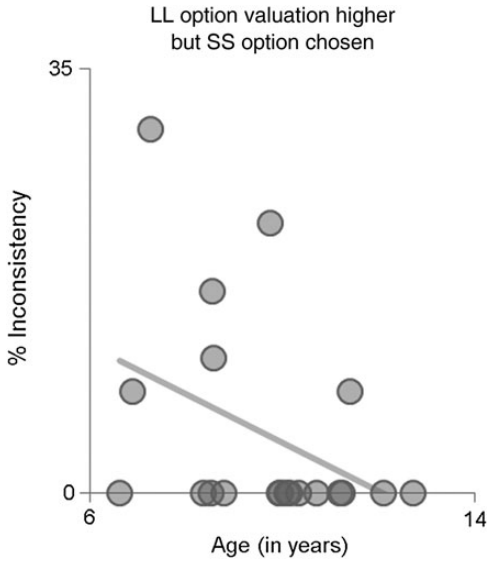

Figure 2. Percentage of inconsistency between valuation and choice in younger and older children. There was a significant age-related decrease in yielding to temptation as indicated by less children choosing the SS (small soon) option in spite of valuing it less than the simultaneously presented LL (large late) option with age ($r = -0.392$, $P = 0.048$, one-tailed).

choice inconsistencies in the ICT. Two types of inconsistencies were looked at: first, if subjects switched their choices on a repetition of the same trial type, and second if subjects discount function did not decrease monotonically. No age differences could be found in either type of choice inconsistency ($P > 0.4$ for all). Furthermore, we find a high correlation between the degree of discounting inside and outside the scanner ($r = 0.778$; $P = 0.001$; Supplementary Fig. 1), which suggests stable decisions over different experimental contexts and measurement time points. These data indicate that the reported significant associations between age and intertemporal choice cannot be explained by any age-related increase in the ability to implement decisions without error.

Children were also asked to name personal events that were likely to occur at the 2 end points of the future temporal dimension tested (i.e. in 4 and in 56 days). Each and every child was able to name at least one event for each time point (i.e. attending a soccer game; Easter holidays), the likelihood and truthfulness of which was checked with the accompanying parent of the child. There was no age-related change in naming an event for any time point (χ^2 test; $P = 0.99$). This shows that all children were equally capable of imagining concrete events in the future within the temporal range of delays employed in our choice and valuation paradigms.

Functional Activation and Effective Connectivity During ICT and VT, and its Modulation by Age and Behavioral Control

To explain the observed developmental change of intertemporal choice in terms of underlying neural mechanisms, we analyzed fMRI data acquired during the VT and the ICT. We found activation in the vmPFC to be parametrically modulated by subjective value both during the VT ($x = 6$, $y = 44$, $z = -8$, $P_{svc} = 0.05$; Fig. 3*A*) and during the ICT ($x = 6$, $y = 47$, $z = -14$, $P_{svc} = 0.05$; Fig. 3*B*). Importantly, when performing the analysis for the ICT when covarying out which option was chosen

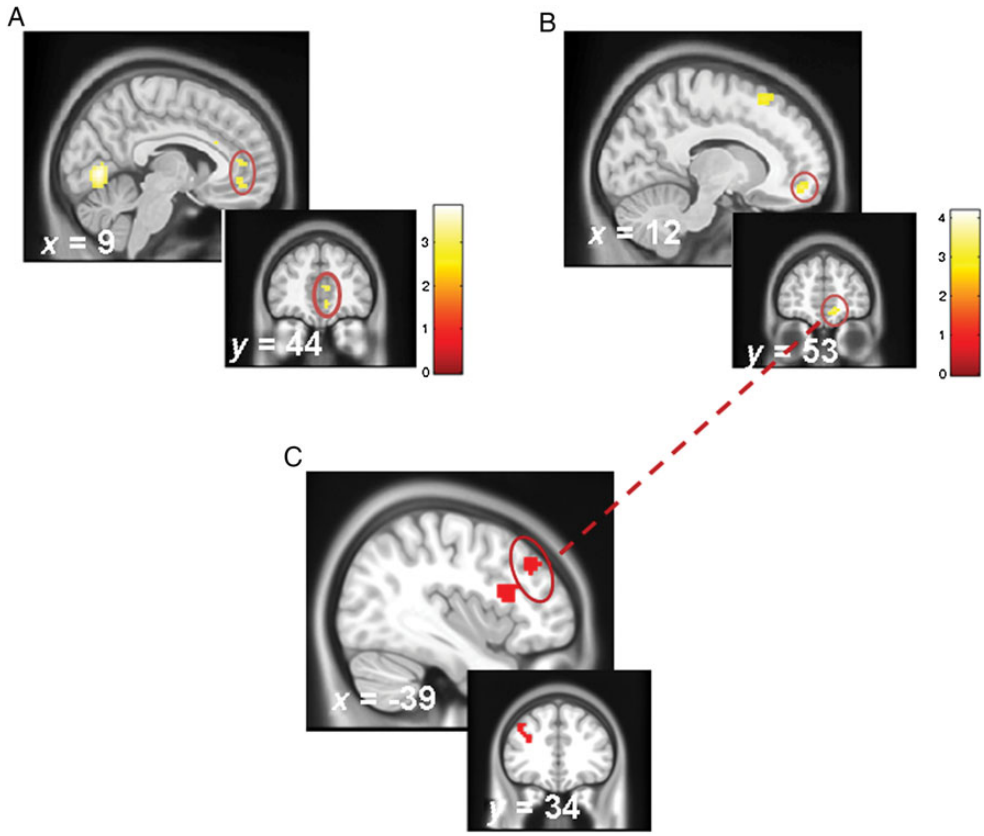

Figure 3. fMRI data acquired during valuation and ICTs. (*A*) Activation in the vmPFC correlated significantly with subjective valuation of individually presented options during valuation ($x = 9$, $y = 44$, $z = -8$, $P_{svc} = 0.05$; Supplementary Material) and (*B*) during choice ($x = 12$, $y = 53$, $z = -11$, $P_{svc} = 0.05$; Supplementary Material). (*C*) Using activity in the vmPFC as a seed region, greater functional connectivity was found with lDLPFC as a function of age, impulse control, and temporal discounting (displayed overlap in red at: $x = -39$, $y = 34$, $z = 20$, $P_{FWE} = 0.05$; Supplementary Material).

at the first-level analysis, this activation in the vmPFC persists ($x = 3$, $y = 44$, $z = -14$, $P_{svc} = 0.05$; Supplementary Table 9). This shows that our paradigm successfully recruited brain regions typically engaged in the valuation of rewards both in the context of our valuation and our choice paradigm. There were no correlations between activity in any brain regions and individual differences in temporal discounting or age, neither during the VT nor during the ICT.

The control-integrated valuation hypothesis predicts that, during the ICT, age-related changes ought to be observed in the functional coupling between valuation signals in the vmPFC with brain areas dedicated to behavioral control, such as DLPFC. To test for this, we conducted a connectivity analysis from the vmPFC comprising voxels, which were modulated by subjective value during choice. We found that functional coupling between vmPFC and left DLPFC indeed increased with greater patience, as measured by the AUC ($x = -27$, $y = 20$, $z = 22$, $P_{FWE} < 0.05$; Fig. 3*C*). Furthermore, vmPFC–DLPFC coupling also increased as a function of age ($x = -30$, $y = 23$, $z = 19$, $P_{FWE} < 0.05$; Fig. 3*C*) and crucially also with individual differences in implementing behavioral control, as indicated by performance in the SSRT ($x = -36$, $y = 26$, $z = 16$, $P_{FWE} < 0.05$; Fig. 3*C*). Furthermore, we show that the modulation of vmPFC–DLPFC connectivity by increased patience and age and behavioral control (the latter albeit at an uncorrected statistical threshold of $P < 0.005$) occurred particularly in those trials in greatest need of intervening control processes, namely where the difference in subjective value between the future and the immediate option was small as opposed to large and not at all in those trials where the subjective value of the future option was already much larger than that of the immediate option (Supplementary Material).

These data confirm the predictions of the control-integrated valuation hypothesis and suggest that age-related changes in intertemporal choice occur as a result of a developmental change in value signals integrating information from brain regions dedicated to behavioral control.

Mediation Analysis

Given the significant associations between SSRT scores, functional coupling between vmPFC and left DLPFC, and our measure of temporal discounting during choice, we sought to assess if age-related changes in temporal discounting are mediated by concomitant changes in behavioral control and vmPFC–DLPFC coupling. To do so, we performed a mediation analysis, with age as a dependent variable, temporal discounting as an outcome variable, and SSRT scores and functional coupling as multiple mediators. Analyses were conducted using bootstrapping procedures recommended for multiple mediators and operationalized in an SPSS Macro (Preacher and Hayes 2008). We used 20 000 bootstrap resamples of the data with replacement. Statistical significance with alpha at 0.05 is indicated by the 95% confidence intervals not crossing zero. We found a significant total mediation effect of behavioral control and vmPFC–DLPFC coupling with respect to the

relationship between age and temporal discounting (indirect effect 2.35, SE = 1.52, 95% confidence intervals: 0.276, 6.361; Fig. 4). This last finding suggests that age-related changes in intertemporal choice are mediated by concomitant developmental changes in a cognitive process related to behavioral control subserved by the functional integrity of a neural network comprising left DLPFC (lDLPFC) and vmPFC.

Cortical Thickness

Our measure of cortical thickness correlated neither with age nor with any of our behavioral variables.

Discussion

Behaviorally, our findings suggest that developmental change in behavioral control is a critical ingredient in bringing about the observed age-related changes in intertemporal choice. This is indicated by a significant correlation between age and temporal discounting during choice but not during valuation, and that these observed age-related changes during choice are accompanied by changes in the ability to inhibit prepotent responses in an independent motor control task. Furthermore, younger children show a greater susceptibility to yield to temptation by choosing immediate rewards despite valuing them less than the delayed alternative. The absence of any evidence, suggesting an age-related decrease in decision errors (i.e. choice inconsistencies over sessions), buttresses our claim that developmental changes in behavioral control constitute a genuine developmental mechanism accounting for observed changes in intertemporal choice. Neurally, vmPFC tracks a subjective value of presented options both during valuation and choice; however, only during choice is there functional coupling with brain regions implicated in behavioral control, such as DLPFC. Crucially, the extent of vmPFC–DLPFC functional coupling increases with reduced temporal discounting during choice, as well as age and motor control. These findings suggest that age-related changes in behavioral control and underlying neural networks represent a unique developmental mechanism accounting for the improvements in the ability to forego immediate pleasure, regardless of any choice-independent valuation processes.

Our finding of age-related changes in intertemporal choice and its link to the functional integrity of cortical systems dedicated to integrating value signals from distal brain regions, such as the left DLPFC, can potentially be explained in terms of the delayed maturational processes of this region. The DLPFC is one of the brain regions latest to mature (Sowell et al. 2001; Gogtay et al. 2004). Even though we found no association between age and cortical thickness in our sample of children, other changes comprise an increase in structural connectivity between cortical regions (Lebel and Beaulieu 2011), leading to more efficient functional connectivity over an increasingly widely distributed range of regions (Hagmann et al. 2010), particularly for frontal regions (Fair et al. 2007; Raznahan et al. 2011). Thus, the development of temporal discounting and particularly the ability to forego immediate pleasure during childhood could be attributed to the maturation and associated functional integration of lDLPFC, a region already known to play a critical role in implementing behavioral control in the context of complex and particularly intertemporal choice in adults (Hare et al. 2009; Figner et al. 2010) and adolescence (Christakou et al. 2011; Schilling et al. 2012).

The correlation of functional connectivity between vmPFC and lDLPFC and our measure of behavioral control is compatible with the view that vmPFC computes an integrated value signal that necessarily integrates input from distal neural sources, including ones relevant for behavioral control (Hare et al. 2009; Figner et al. 2010; Kable 2010). This process appears to undergo functional change with age in the context of choices requiring behavioral control. Behavioral control may function as a mechanism that exerts its influence in making future options appear more valuable during choice, an influence that can only be exerted if the functional pathways between these regions are fully matured. Further studies comparing specific versions of the control account in intertemporal choice may shed light on the precise mechanism of control (e.g. modulation of attention). One intriguing recent proposal suggests that, given that behavioral control implies costs in terms of effort, there may also be a value signal attached to self-control (Kool et al. 2010, 2013). Whether such an explanation can also account for age-related changes in temporal discounting requires further empirical tests. As they stand, our data provide evidence that the development of self-control, as measured by the ability to inhibit a prepotent response, plays a

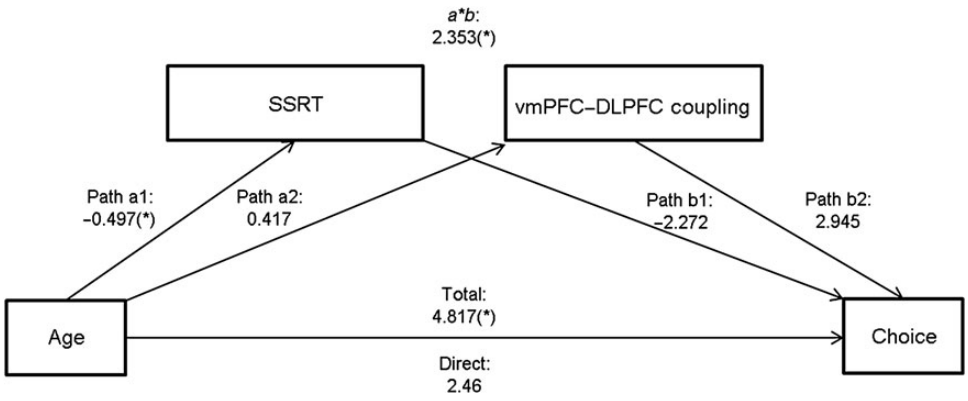

Figure 4. Mediation models for the effects of age on intertemporal choice via behavioral control and vmPFC–DLPFC coupling. Values are standardized regression coefficients, and asterisks indicate significant coefficients (*$P < 0.05$). Age-related changes in behavioral control and associated vmPFC–DLPFC coupling during intertemporal choice mediate developmental changes in intertemporal choice.

crucial role in observed age-related changes in intertemporal choice, and that this is played out also at the neural level, whereby brain regions involved in implementing behavioral control are increasingly recruited during intertemporal choice.

Another way of addressing this question is comparing neural activation when choosing the delayed option compared with the immediate one and vice versa. However, given the age-related differences in the number of say choosing the delayed option, where with increasing age there is an increasing number of trials of delayed choices compared with immediate choices, this automatically means that the signal-to-noise ratio of delayed trials is in favor of older children and of immediate trials in favor of younger children. Given that we are specifically interested in age-related differences in intertemporal choice and developmental changes in brain regions subserving this, not biasing this in terms of analyzing specific decisions seemed like the most optimal strategy. Given that some children only ever chose immediate rewards or delayed rewards only, selecting this amount of trials for all children was not an option. Whereas this may not be the most ideal in terms of understanding the specific neural mechanism underlying specific choices, it does provide a measured and unbiased estimation of the development of brain regions involved in explaining age-related changes in intertemporal choice. To do so, future studies should optimize their design such that a sufficient number of trials can be obtained for either type of decision across a tested age range.

Whereas an association between temporal discounting and other measures of impulse control such as the SSRT is not always found in adults (Broos et al. 2012), the present sample of children shows a strong correlation between the 2 measures. Such a functional overlap of behavioral control in the context of a simple motor task and a cognitively more complex temporal discounting task observed in the present sample might be explained with reference to theories on the differentiation of cognitive abilities during development (Tucker-Drob 2009). Thus, implementing behavioral control during childhood in the context of various tasks may recruit the same neural structure, in this case left DLPFC, which during the course of development becomes both functionally and neural differentiated, a process echoed in the literature on the development of general executive functions (Rhemtulla and Tucker-Drob 2011; Wiebe et al. 2011; Lee et al. 2013).

Some issues arose from this study that future work may wish to address. Even though the use of a valuation and a choice task allows one to compare consistency of behavior between the 2, there are differences between the 2 tasks other than choices made or not, such as presenting 1 versus 2 options, which in turn could have an effect on the behavior displayed (i.e. valuation and choice). It is unlikely, however, that behavioral control ought to lead to such striking differences in age-related changes and task performance, making this difference in how the options were presented an unlikely candidate to account for our developmental findings.

Taken together, the present work provides novel insights into the developmental cognitive and neural mechanisms underlying age-related changes in intertemporal choice during childhood. We show that the development of neural networks dedicated to implementing behavioral control constitutes the driving ontogenetic force behind age-related changes in future-oriented economic decisions. This mechanism helps children to increasingly overcome the temptation of less valued but immediately available rewards. More generally, these findings suggest that the primary reason why younger children behave impatiently is not because they value immediately available rewards so much more, but rather because they cannot implement patient choices in the moment of making a decision (Steinbeis et al. 2012). This inability may have its roots in the late maturation of the prefrontal cortices, which subserve the capacity for impulse and behavioral control. Given the enormous personal and economic costs associated with impulsive behavior, including poor health, undersaving, and clinical conditions such as addiction, understanding the mechanisms of this behavior early in life is crucial, since increased plasticity allows room for interventions with long-lasting efficacy.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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Notes

Conflict of Interest: None declared.

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