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Moderators of the association between brain activation and farsighted choice

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ABSTRACT

There is equivocal support for the hypothesis that preference for later larger (LL) over sooner smaller (SS) monetary alternatives (e.g., $50 in four months over $30 today) is associated with functioning of the insula and the prefrontal cortex (especially the lateral PFC). In the present study, we re-examined overall neural correlates of choice using a procedure to minimize potential confounds between choice (which is necessarily not under experimental control) and valuation. In addition, we assessed whether choice-related brain activity is moderated by 1) overall level of delay discounting and 2) the degree of stochasticity in individuals' intertemporal choices.

Twenty-one participants completed an individualized intertemporal choice task while brain activity was measured using functional Magnetic Resonance Imaging (fMRI). Across participants, LL choice was associated with activity in left dorsolateral prefrontal cortex (dlPFC), left insula/inferior frontal gyrus (IFG), frontal pole and the anterior cingulate cortex (ACC). Stochasticity positively moderated the LL>SS activity within the left insula and left IFG. Degree of discounting also interacted with choice related activity, but only outside the LL vs. SS main effect map (in the posterior cingulate cortex, and precentral/postcentral gyrus and left dlPFC). Main effect results are consistent with the notion that lateral prefrontal activity during intertemporal decisions bias selection in the direction of LL. Correlation findings indicate that choice related activity in the left insula and IFG is moderated by the stochasticity of intertemporal choices, and may reflect reduced "executive function" demands among highly consistent participants.

Introduction

More so than other species by a great margin, human behavior is intentionally directed at shaping temporally distant outcomes (Gilbert, 2006). *Delay discounting* laboratory tasks assess the limits of this future-orientation by presenting research participants with choices between rewards (often monetary) that vary in size and immediacy (e.g., "Would you like $5 today, or $10 in 1 month?"). An individual participant's behavior is then typically characterized by deriving a *discount function* that models the effect that, for him or her, *delay* has on *value*. Although the paradigm has been criticized as not capturing some important features of real-world intertemporal decision-making where trade-offs are rarely so discrete and explicit (Rick and Loewenstein, 2008), the steep discounting observed among groups exhibiting real-world temporally myopic behavior (e.g., drug addicts, compulsive shoppers, and individuals with gambling problems (Bickel, 2001; Critchfield and Kollins, 2001)) provides some evidence for construct validity. The task has reasonably high stability (test–retest correlation = .71 across a 1-year span (Kirby, 2009)).

Intertemporal decision-making is stochastic, which is to say, particular choices are only probabilistically related to modeled discounted value. When the modeled values of an SS and LL alternative pair are not far apart, the lower modeled value alternative will be chosen on some minority of trials. Discount functions predict preference between intertemporal alternatives, but they do not directly predict the consistency of that preference (e.g., whether it will be 60%, or 99%). Stochasticity can be characterized with a second layer of modeling that maps the consistency of preference as a function of the distance in discounted value of the alternatives. At least conceptually, the level of stochasticity in an individual's intertemporal choice behavior is orthogonal to his or her overall modeled discounting (i.e., a steep discounter can exhibit high or low stochasticity, as can a shallow discounter).

It has been widely hypothesized that LL choice is associated with activity in the lateral prefrontal cortex, and especially the dorsolateral PFC (dlPFC). This hypothesis rests at least in part on the idea that the presence of an SS presents an "executive control" challenge that is met when an LL alternative is instead selected (e.g., Bickel et al., 2007; Boettiger et al., 2007; McClure et al., 2004; McClure et al., 2007).

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To the extent that LL choice implicates deployment of executive control, an association with brain activity in areas within the lateral PFC could be predicted from the extensive literature linking the region to goal-directed biasing of behavior (Miller and Cohen, 2001), to planning (Fincham et al., 2002) and to intentional suppression of prepotent but goal-inappropriate responses (Aron et al., 2004).

A rapidly growing collection of studies pair delay discounting tasks with neuroimaging (for reviews, see Carter et al., 2010; Monterosso and Luo, 2010). Several of these have investigated whether brain activity during decision-making predicts the individual's intertemporal choices (Christakou et al., 2011; McClure et al., 2004; Rubia et al., 2009; Weber and Huettel, 2008; Wittmann et al., 2007). Although consistency across these studies is modest, two of the four studies that reported whole-brain analyses of the contrast between LL and SS choices observed an association between LL choice and more activation within the dlPFC (inclusive of BA9) (Christakou et al., 2011; McClure et al., 2004; Weber and Huettel, 2008). There is also support from multiple studies of an association between choice of LL over SS and greater activity in the posterior insula. This was most strongly observed (and bilaterally so) in Wittmann et al.(2007). The importance of the posterior insula in LL choice is also suggested by a study of reward-based learning (Tanaka et al., 2004), in which posterior and anterior portions of insular were preferentially recruited during responses consistent with LL reward pursuit (relative to SS reward pursuit).

A careful synthesis of the available evidence across existing studies would need to focus on a number of complicating factors including procedural variation, modeling variation, and inconsistency in anatomical labeling, and is beyond the scope of this paper. But we draw attention to one data modeling issue that is particularly relevant here, and that is the consideration of *value*. If there are brain regions that track the present-value of *chosen alternatives* (which is consistent with Kable and Glimcher, 2007), these regions would be associated with LL or SS choice if *value* differs systematically between SS and LL in a given study. And since choices are not under experimental control, and presumably are related to valuation, there is no perfect solution to ensure equal value between SS and LL choices. This problem is minimized by adaptive procedures that adjust the values of alternatives based on the participant's choices such that SS and LL values are never far apart. However, if an adjusting procedure is used and only the SS is adjusted in successive trials (as in the Christakou et al., 2011; Rubia et al., 2009; Wittmann et al., 2007), value will tend to be greater for SS selections. The reason is that SS selections will be made predominantly when the SS has a value that is greater than that of the fixed LL. To make concrete, suppose LL is fixed at $100, and repeatedly presented to a participant for whom its present-value is precisely (and with no stochasticity) $38. When offered an SS<$38, she always chooses the LL. When offered an SS>$38, she always chooses the SS. For this participant, the mean present-value for all LL choices will of course be exactly $38 (the present value of the fixed LL). The mean present-value for all SS choices will be higher, since this option is selected only when SS>$38. Therefore a direct contrast of brain activity of SS vs. LL choice trials may identify value tracking regions unrelated to choice. While this example is a simplification, incorporating participant stochasticity and more complicated procedures for generating LL alternatives does not change the nature of this systematic mismatch in value if only the SS is adjusted during titration.

Alternatively, value can be included as a regressor as done in Weber and Huettel(2008). This reduces the effect that value-related signal has on the SS vs. LL contrast. However, deviations from linearity in the relationship between value and MR signal can limit the effectiveness of this purely statistical approach when there is a large mismatch in value between SS and LL choices, as can occur when alternatives are not tailored to the individual's discounting behavior. More importantly, without tailoring alternatives to individual discounting, the collinearity observed between value and choice will vary as a function of the individual's level of discounting in relation to the set of questions asked. And since collinearity with other regressors entails loss of statistical power, the contribution any one individual makes to group level statistics will depend on her discounting behavior. Therefore, we think a better approach combines the above methods, both utilizing an adaptive procedure so that the mismatch in value between SS and LL choices will be small and independent of overall discounting behavior, and additionally including a value regressor to "partial out" remaining covariation between value and choice.

The first goal of this report is to re-assess the association between LL choice and brain signal change in a manner that reduces the potential for differential valuation to affect results. In order to do this, we included an adaptive choice procedure designed to minimize value discrepancies between SS and LL choices, while *also* including modeled valuation as a regressor in analyses. Our second goal is to assess whether individual variation in the level of stochasticity and/or the level of delay discounting moderates the associations between LL choice and brain activity. With regard to stochasticity, informal feedback suggested that participants approached the task differently, with some but not all relying on rules (as in a participant who said he always went for the immediate money unless he got twice as much for waiting). For a participant who based her responses at least in part on a systematic algorithm, stochasticity would generally be low (depending on the relationship between the algorithm and the modeling utilized). Further, we hypothesized that for such a participant, lateral PFC recruitment associated with LL choice would be attenuated. At the limit, a complete algorithmic orientation to the task can transform each question into a math problem, and executive function would not causally contribute to whether the answer to that math problem favors SS or LL (though there may be differentiation subsequent to becoming aware of whether the answer favors SS or LL). Our hypothesis that shallow discounters (for whom LL choice required forgoing a large immediate alternative) would exhibit relatively low prefrontal LL>SS signal is perhaps counterintuitive, but it is consistent with recent findings. We previously presented research participants with opportunities to win the individual rewards that comprised an intertemporal "indifference pair" (i.e., an SS and LL pair that were equally preferred). We found that the SS reward recruited greater response than the LL in regions that track value. This implies that the choices participants had made were temporally far-sighted, relative to the value-tracking responses that the rewards elicited when individually presented. The tendency to make choices that are more farsighted than would be predicted by valuation outside of a decision context was *more* pronounced among cigarette smokers (Luo et al., 2011), a group that generally exhibits steep discounting (Baker et al., 2003; Bickel et al., 1999; Mitchell, 1999). Taken together, these data suggest (again, counterintuitively) that the involvement of executive control functioning during LL choice may be greater among individuals that discount steeply. Perhaps the individual with little tendency to discount tends also to have little incentive to engage cognitive control strategies during an intertemporal choice task.

To test the above hypotheses, we developed a procedure in which all participants were required to make a series of intertemporal choices that ranged from those in which the SS option was just sufficiently large to elicit 100% preference, to those in which the LL was just sufficiently large to elicit 100% preference. This choice environment allowed us to assess overall discounting and stochasticity, in a setting in which brain activity recruited during difficult intertemporal choices would be evident. In order to minimize the extent to which analyses were dependent on particular modeling choices (e.g., hyperbolic vs. exponential), all choices were between an immediate and a four-month delayed amount, and the amounts

varied across trials within two relatively narrow amount ranges, each of which was modeled separately.

Material and methods

Participants

Twenty-one healthy volunteers participated in the study. They gave written informed consent to all experimental procedures (approved by the Institutional Review Board of the University of Southern California) and were paid for participation. All participants were right-handed, had normal or corrected-to-normal vision, and were free from any psychological and neurological disorders. Among the 21 subjects included in analyses, 13 were female. Ages ranged from 22 to 44 (mean = 29.9 ± 6.1).

Overview of delay discounting task

We obtained fMRI data while participants performed an individualized intertemporal choice task. After extensive pre-scan testing (described below), participants completed an adaptive intertemporal choice task in the scanner. All alternatives were specified temporally as either "today" or "in four months." Participants were instructed that one of the trials from the task would be randomly selected, and that they would receive the alternative they chose for that trial in the form of a Visa gift card. They were further instructed that if the alternative they selected had an associated delay, the Visa gift card would not become activated until the specified day. Participants were informed that they could get a replacement if they lost their card during the intervening delay (and that if this occurred, the original card would not be activated).

Discrete choice modeling of discounting behavior

For modeling purposes, we treated each alternative as having just two attributes, *Amount* and *Delay*. A common approach to modeling delay discounting is to estimate a discount function that translates delayed amounts into present value, such as:

$$V = \frac{A}{1 + Dk} \tag{1}$$

where V = time discounted value (i.e., "present value") of a delayed amount, A = amount, D = specified Delay, and k is a fit parameter (Mazur, 1987). Although we used this model, it should be noted that it assumes (unrealistically) a linear relationship between Amount and Value; concavity in the actual mapping from Amount to Value will result in inflation of estimation in the discount parameter k (Ho et al., 1999; Pine et al., 2009; Pine et al., 2010). We will return to this issue later. The model also does not allow for the systematic tendency to discount less steeply when rewards are greater in magnitude (Loewenstein and Prelec, 1992). To minimize the effect of this, we included two separate models for each participant, each within a narrow range of reward magnitudes, described below.

Since the only delay used in the present study was four months, we treated the Delay as a single period. In other words, D = 1 if an amount was delayed by four months and D = 0 if it was not delayed. For any immediate versus delayed alternative pair, there is some value of k that makes the two amounts present-value equivalent, which is the value of k that satisfies

$$V(A_i) = V(A_d)$$

or

$$A_i = \frac{A_d}{1 + k} \tag{2.1}$$

where A_d, A_i are the delayed and immediate amounts, respectively. We will refer to this value throughout as the "equivalence-k" or "k_e". Rearranging Eq. (2.1), we obtain:

$$k_e = (A_d - A_i) / A_i \tag{2.2}$$

Note that k_e is a property of an SS vs. LL alternative pair rather than of the individual's behavior. If k^* represents the value that, using Eq. (1), characterizes an individual's underlying tendency to discount (that is the value of k that satisfies P(LL) = 50%) then she will generally choose the LL option if $k_e > k^*$ and the SS option if $k_e < k^*$. However, actual choice will sometimes be at odds with predicted preference, particularly when k_e and k^* are similar. We used the logit model (Cramer, 1991) to describe the probability of choosing the LL alternative, as a function of k_e, as follows:

$$P(LL) = \frac{1}{1 + e^{-(\alpha + \beta k_e)}} \tag{3}$$

in which α and β parameters are used to specify the relationship between the k_e associated with a given alternative pair and an individual's probability of choosing the LL. The parameter β captures the marginal effect of a one unit increase in k_e and reflects the stochasticity of individual performance; the larger the β, the less stochastic. The parameter α represents the mean of all other relevant observable factors not explicitly included in the model. The parameter estimates were calculated in MATLAB by maximum likelihood estimation, using the Newton–Raphson method. The same analysis was additionally carried out using a probit function, for purposes of comparison.

A post-hoc "model-free" stochasticity analysis was additionally performed in which we identified occurrences (by chance) of multiple presentations of the same alternative pair to a particular participant. We anticipated that these occurrences, since fairly rare and unsystematic in terms of distribution within the participant's adaptation window, could not be used as a measure of individual level of stochasticity. These data, however, do provide a point of contact between modeled and model-free stochasticity. Mainly, we examined the degree to which the level of stochasticity predicted for these alternative pairs by the subject-specific logit models corresponded to observed inconsistency in response to the repeated alternative pair. In order to avoid circularity, for each test point, the repeated trials were removed and a subject-specific logit model was re-estimated in order to derive the predicted likelihood of inconsistency. In other words, we asked, *do the logit models of stochasticity predict when the participant responds to the same alternative pair differently on different occasions?*

Pre-scan testing

The subject-specific estimates of discounting behavior prior to scanning were based on two procedures. First, participants completed a brief (27-item) computerized version of the Monetary-Choice Questionnaire, developed by Kirby et al. (1999). This allowed for an initial "rough estimate" of individual level of delay discounting. Based on these data, two k-parameters were estimated for each participant, corresponding to discounting within each of the amount ranges to be used in the study ("Low Range" was $21 to $35 and "High Range" was $51 to $65). These initial estimates of discounting were used as the starting point for the second pre-fMRI delay discounting task, which was an adaptive discounting procedure. The adaptive discounting procedure was directed at refining subject-specific estimates. During the adaptive discounting procedure, participants were presented with intertemporal choices consisting of one option that was delayed by four months and a second option that was immediately available. The delayed option amounts were random draws from a uniform distribution within the two amount ranges (low and high). The

immediate amount was the amount that would be equally preferred given the current titration k-value (denoted k_e) for the corresponding amount range. This was determined by solving for A_i of Eq. (2.2). The k_e value was adjusted up a quarter $\log_{10}$ step after an SS choice and down a quarter $\log_{10}$ step after an LL choice (separately within each amount range) until the stability criterion was reached. Stability was operationalized as a window of eight trials in which k_e did not deviate by more than two steps (three values). This criterion was assessed separately for each amount range, and no further pre-fMRI questions were presented within an amount range once the criterion was satisfied. Failure to reach criterion for both amount ranges after eight minutes was considered exclusionary, but did not occur during the study.

Adaptive discounting task during fMRI

The fMRI discounting task was identical to the adaptive discounting task described above except for trial duration and the presence of control trials. As in the pre-scanning adaptive choice task, on each intertemporal choice trial participants were presented with a choice between an LL and SS. Intermixed with the intertemporal choice trials were "control choice" trials (12 of 38 trials in each task run) in which one alternative dominated the other by being superior on amount, and equivalent on delay. Analyses related to "control choice" trials are not relevant in the present report. Intertemporal choice trials were generated using the identical procedure to that used in the pre-scan adaptive choice procedure (described above). As in the pre-scan adaptive procedure, k_e was initially set to the subject-specific best-fit parameter (here based on preference during the pre-scanning adaptive procedure). Again, k_e was adjusted after each choice separately for the High Range and Low Range reward trials which were interleaved.

The two reward alternatives were presented on either side of the screen separated by a line, and side was randomized. Participants were instructed to choose between the two options by pressing a left or right button on a response pad. The participant was free to respond at any time during the trial, and the text of the option they chose changed from white to yellow after their response and remained on the screen until a total of 8 s had elapsed since presentation. After 5 s, if a response was not recorded, the instruction "Please Respond" appeared. After 8 s, the trial ended even if a response was not recorded. During each run of the task, there were 26 intertemporal choice pairs and 12 control choice pairs, resulting in 304 s running time. Participants were instructed that one of the trials would be randomly selected at the end of the task, and that they would receive whichever option they selected for that trial (available after the indicated delay). Each participant completed two functional scans separated by one structural scan (4 min). There were a total of 52 intertemporal choice pairs and 24 control choice pairs for each participant. For the purposes of the present analysis, it is important to note that because of the nature of the Adaptive Discounting Task, each individual was presented with a set of alternative pairs with associated k_e values that ranged from just sufficiently small that the individual always chose the SS, to just sufficiently large that the individual always chose the LL, with the majority of trials based on k_e values that elicited both SS and LL selections.

Because of the adaptive nature of this task, some participants might become aware of the endogenous basis by which alternative pairs were generated. Such a participant might have selected more LL choices in order to drive up the magnitude of available SS alternatives. To make concrete, a hypothetical individual that only actually valued immediate money might make LL selections in order to keep the immediate amount from adapting down towards $0. To assess the likelihood of this, we compared discounting during Kirby's fixed choice set with discounting during the adaptive choice procedure. If there was gaming in the adaptive choice procedure, responses should diverge, with greater LL preference during the adaptive relative to the fixed-choice procedure.

MRI acquisition

MRI data were collected in the Dana and David Dornsife Cognitive Neuroscience Imaging Center at USC using 3T Siemens MAGNETOM Tim/Trio scanner with a standard birdcage head-coil. Participants laid supine on a scanner bed, viewing stimuli through a mirror mounted on head coil. Blood oxygen level-dependent (BOLD) response was measured by echo planar imaging (EPI) sequence with PACE (prospective acquisition correction), TR = 2 s, TE = 30 ms, flip angle = 90°, FOV = 192, in-plane resolution = 64 × 64. A total of thirty-two axial slices were used to cover the whole brain with no gap. The slices were tilted 30° along anterior commissure–posterior commissure plane to gain better signal in orbital frontal cortex. Anatomical images (256 × 256 × 176) with 1 × 1 × 1 mm^3 resolution used a T1-weighted three-dimensional magnetization prepared rapid gradient echo (MP-RAGE) sequence (inversion time, 900 ms; repetition time (TR), 1950 ms; echo time (TE), 2.26 ms; flip angle, 90°).

fMRI analyses

fMRI data were analyzed using FEAT (fMRI Expert Analysis Tool) version 5.98, part of the Oxford University Centre for Functional MRI of the Brain (FMRIB) Software Library (www.fmrib.ox.ac.uk/fsl). Structural images were realigned and warped, normalized into standard space [Montreal Neurological Institute (MNI)] using affine transformation (Jenkinson and Smith, 2001). Before functional images were entered into GLM, they were motion corrected by MCFLIRT (Motion Correction using FMRIB's Linear Image Registration Tool) (Jenkinson et al., 2002), temporarily filtered by a high-pass filter with 100 s cutoff and spatially smoothed by a Gaussian kernel of full-width at half-maximum of 5 mm.

The decision-making period was modeled parametrically (for the epoch beginning with the presentation of the alternatives and ending at the moment a selection was recorded) using three variables: 1) the reaction time for the trial, which we computed as the time between the presentation of the alternatives and the participant's response (RT), 2) the time-discount value of the chosen alternative (Value), and 3) Choice (LL over SS). With respect to including RT, we reasoned that the modeled epoch contained functionally distinct processes including reading, processes involved in decision-making, and execution of the motor response. Since we expected recruitment devoted to reading and to execution of the button press to vary less across trials than processing related to decision-making, we expected this regressor to be associated with activation related to decision-making (although this is not a critical assumption). For our Value regressor, we computed the value of the chosen alternative, discounted using k^* which was estimated based on overall preference data (Eq. (1)). For the Choice regressor, LL was coded as 1 and SS coded as 0.

Signal change associated with the Choice regressor was subjected to a covariate analysis across participants based on 1) individual degree of discounting, and 2) individual degree of stochasticity (β from Eq. (3)). Perhaps because response to variation in k_i is logarithmic (indifference pairs based on $k_i = .001$ and $k_i = .002$ are more psychologically different than pairs based on $k_i = .101$ and $k_i = .102$) β, a measure of the slope of change in response as a function of change in k_i, tends to be lower for participants whom discounted more steeply. Therefore, for analyses of stochasticity, β was replaced with residuals after partialing out the relationship with normalized k^*.

We ran additional parametric analyses to address potential competing accounts of findings. First, the primary analyses were rerun, this time including Value of unchosen alternative in the model (in addition to RT, Value of chosen alternative and Choice). This was

done to assess whether Value of unchosen options could be a basis for an observed correlation between k^* and LL–SS findings (see below). The unchosen alternative and chosen alternative were similarly valued in our design, since the adaptive procedure kept alternatives near the prevailing indifference point. So in our model, the value of the unchosen option was orthogalized to the value of the chosen alternative, so that common variance shared between them would go to the chosen alternative value of the regressor. Critically, neither value regressor was orthogonalized to Choice. Second, primary analyses were rerun, this time including Amount of chosen alternatives, Choice and RT (but not Value). In our study, LL options were similar across subjects, but SS options were higher for shallower discounters. These analyses were done to identify whether regions associated with LL might be interpretable not as relevant to intertemporal choice *per se*, but rather as amount tracking regions (since amounts are higher for LL alternatives). With this additional analysis, we could assess whether the LL–SS clusters reported in the primary analysis tracked Choice or Amount, once the variance common to both was excluded.

For the above analyses, each predictor was convolved with canonical double gamma hemodynamic response function (HRF) and temporal derivatives were added as well. A fixed-effect model was used for cross-run analysis by forcing the random effects variance to zero in FLAME (FMRIB's Local Analysis of Mixed Effects) (Beckmann et al., 2003). Cross-run analysis results were input to group-level analysis using a mixed-effects model (Woolrich et al., 2004).

Results

Behavioral results for the adaptive choice procedure

Overall, the LL was chosen on 51.01% of trials across all participants. The mean deviation from a perfect 50%–50% split in choices was 4.1% (SD = 3.3%). RT did not differ between trials participants chose LL vs. SS ($t = -1.648$, $p = 0.115$, with means in the direction of longer RTs for SS choice). Treating delay as 120 (days) rather than 1 (period) for purposes of comparability with other reports, the best-fit k-parameter was .00227, .0112, .0255 for the 25th, 50th, and 75th percentile participants for the High Range reward ($53 +/− $7 delayed by 4 months vs. the immediate amount generated by the adaptive procedure) and .00328, .0111, and .028 for the 25th, 50th, and 75th percentile participants for the Low Range reward ($28 +/− $7 delayed by 4 months vs. the immediate amount generated by the adaptive procedure). Thus the median participant was indifferent between $53 in 120 days and $23 now, and between $28 in 120 days and $12 now. Discounting of High and Low Range rewards did not differ significantly ($Z = .261$, $p = .794$ based on Wilcoxon Signed Ranks Test). The best-fit k-parameter from the adaptive procedure did not differ significantly from Kirby's fixed set Monetary Choice Questionnaire ($t(20) = 0.88$, $p = 0.389$).

For the logit model (Eq. (3)), the best-fit β-parameter for the 25th, 50th, and 75th percentile participants was 1.14, 2.98, and 12.61 for the High Range reward, and 1.08, 3.91, and 7.30 for Low Range reward. The alternative probit function model yielded stochasticity estimates with nearly identical distributions to the logit model ($r > .99$) and so we report only on the logit model.

Across all 21 participants, there were 209 instances in which the same participant was presented with the identical alternative pair on more than one trial (never consecutively). Among these, the participant responded inconsistently in 29.7% of the sets. For all repeating pairs, predicted probability of inconsistency (based on the logit model for the participant) was bounded between 0 and .5 (derived from the P(LL)) obtained from the participant's logit model as: $1-(P(LL)^2+(1-P(LL))^2)$. A logistic regression indicated that this index was predictive of whether inconsistency was observed for the repeating pair (Wald = 5.8, $p = .016$).

Imaging findings

Longer RTs were associated with greater signal during decision-making in a network of regions previously identified as associated with difficult (relative to easy) intertemporal choices (Hoffman et al., 2008; Monterosso et al., 2007). This included bilateral activation in the inferior frontal gyrus (IFG), lateral prefrontal cortex (lPFC), anterior portion of the insula, lateral occipital cortex (LOC), as well as anterior cingulate cortex/supplementary motor cortex (ACC/SMC) and parietal cortex. No regions exhibited significantly more activation for shorter RT trials (see Supplementary Fig. 1).

The Value regressor was included as the time discounted value (based on the participant's k^* estimated separately for high and low reward pairs). Increased value was associated with increased signal in the medial PFC (mPFC), bilateral ventral striatum, ACC and occipital cortex (see Supplementary Fig. 2). No regions exhibited significantly more activation in association with lower value choice trials.

Several regions evidenced more BOLD MRI signal during LL choices relative to SS choices (see Table 1). These regions included vmPFC, ACC, frontal pole, left dlPFC and left insula/IFG (see Fig. 1). No regions exhibited greater activation during SS relative to LL choices.

A correlational analysis was performed relating individual discounting (k^*) to the above contrast maps (i.e., LL–SS). Individual discounting rate was positively correlated with brain signal difference in left dlPFC, posterior cingulate cortex (PCC), precentral/postcentral gyrus during LL vs. SS choices (see Table 1 and Fig. 2). However, cluster-level corrected maps of LL vs. SS and correlation with k^* did not overlap.

A second correlational analysis was performed, this time relating stochasticity (β, again, controlling for k^*) to the above contrast maps (again, LL–SS). Individuals exhibiting greater stochasticity in their intertemporal choices exhibited greater recruitment in the left insula and left IFG during LL relative to SS choice (see Table 1 and Fig. 3). The left insula overlapped the cluster identified in the primary LL>SS contrast.

For exploratory purposes, we performed a conjunction analysis to identify voxels that evidenced greater activity ($Z > 2.3$, uncorrected) for both 1) choice of LL–SS and 2) either correlation with k^* (Supplementary Fig. 3) or correlation with stochasticity (Supplementary Fig. 4). Overlapping voxels were observed in the dlPFC, frontal pole and left insula for contrasts 1 and 2, and voxels in bilateral insula, frontal pole, left dlPFC and mPFC evidenced greater activity for both contrasts 1 and 3.

As discussed above, we conducted a supplementary analysis including the present-value of the unchosen alternative (in addition to RT, Value of chosen alternative and Choice). This was done to

Table 1
Whole-brain analysis results for LL vs. SS contrast, and covariate analyses relating individual discounting (K) and stochasticity (β) to the contrast of LL–SS ($Z > 2.3$, $p < .05$, cluster level correction).

	Regions	MNI coordinate	Maximum Z-score
LL–SS	L frontal pole	−48, 40, 2	4.09
	L Middle frontal gyrus/superior frontal gyrus	−34, 40, 34	3.21
	L inferior frontal gyrus	−44, 34, 0	2.99
	L insula/frontal operculum cortex/frontal orbital cortex	−34, 20, 2	3.04
	L central operculum cortex	−46, 0, 8	3.39
	Anterior cingulate cortex	6, 36, −8	3.26
	Ventromedial frontal cortex	4, 44, −16	3.33
K	L middle frontal gyrus	−40, 14, 40	2.98
	Posterior cingulate cortex	4, −28, 26	3.27
	Postcentral/precentral gyrus	60, −12, 26	3.26
β	L insula/frontal operculum cortex	−38, 14, 2	3.03
	L inferior frontal gyrus	−54, 10, 2	2.69
	L central operculum cortex	−42, 4,8	2.97

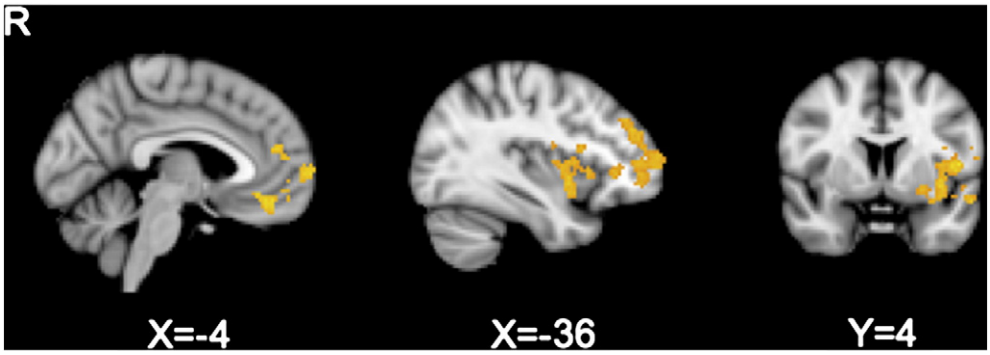

Fig. 1. Areas where signal during LL choices>SS choices with RT and Value included in the model. Significant clusters were observed in the ventromedial prefrontal cortex (vmPFC), anterior cingulate cortex (ACC) frontal pole (FP), left dorsolateral prefrontal cortex (dlPFC) and left inferior frontal gyrus (IFG)/insula. Random-effect model was used for this group-level analysis, and multiple comparisons were corrected at cluster level using Gaussian random field theory (Z>2.3, cluster significance: $p<0.05$ corrected).

assess whether Value of unchosen options could be a basis for an observed correlation between k^* and LL–SS. In this fully orthogonalized model, the uncorrected map for Choice (see Supplementary Fig. 6) was qualitatively similar to that of Choice in the primary contrast (Fig. 1).

Discussion

In delay discounting tasks, participants are free to make their choices by whatever means they wish, and the functional components of the task are, therefore, not fully constrained. As discussed above, one broad area of debate is over whether farsighted choices entail "executive function" such as inhibitory control over prepotent tendency to select immediate rewards or goal-directed biasing of attention towards reward magnitude rather than immediacy. Presently, in a decision environment in which intertemporal choices were tailored to be near the individual's indifference point, choice of a delayed reward over an immediate reward was associated with activation in vmPFC, ACC, frontal pole, left IFG/insula and left dlPFC. These associations between LL choice and greater recruitment in sectors of the PFC are broadly consistent with the "executive function" hypothesis, though of course they are not sufficient evidence for this functional characterization.

LL choice and residual value

As noted in the introduction, we think a complication with regard to several previous reports of LL vs. SS contrasts is that the present value of chosen SS alternatives is higher given an adjusting procedure that moves the SS amount up after LL choices and down after SS choices (Christakou et al., 2011; Rubia et al., 2009; Wittmann et al., 2007). While we presently took methodological and statistical steps to minimize the potential for LL and SS value divergence, we do not think the problem has been fully addressed here (or in any reported LL vs. SS comparison). The level of discounting exhibited on a given trial is likely among the sources of the observed stochasticity in intertemporal choice; on a given trial the participant may discount more or less steeply than typical for her or him. Trials in which discounting is low will be more likely to yield LL choice, and so LL choice trials will be biased towards lower discounting relative to the individual's overall behavior (i.e., $<k^*$). If this is the case, use of k^* to derive present-value will systematically bias in the direction of too low modeled value for LL choices, thereby leaving residual value associated with LL. It is possible that this confound is related to the observed association between LL choice and the vmPFC cluster identified here (which overlaps with the vmPFC cluster associated with the Value regressor). Even at very low and uncorrected thresholds, however, we observed no evidence of value-tracking (based on value regressor analysis) within the dlPFC cluster or left insula/IFG cluster identified in the main LL>SS contrast, and so do not think these findings are plausibly related to value mismatch.

Brain network associated with LL choice

The clusters that were presently associated with LL choice and not with value (in particular the left dlPFC and in left posterior insula/IFG) have both been reported in previous studies. A study in which intertemporal choice questions were not tailored to individual discounting but the present-value of the chosen alternative was regressed (Weber and Huettel, 2008) found that LL choice was associated with greater activation in the left dlPFC (BA 9) cluster with

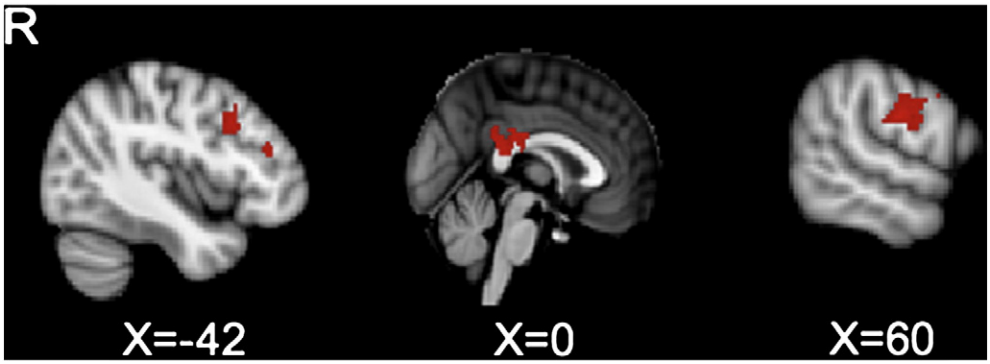

Fig. 2. The contrast of trials where the LL alternative was selected minus trials where the SS alternative was selected was associated with individual variability in discounting. Steeper discounters recruited more LL choice-related activity in the left dorsolateral prefrontal cortex (dlPFC), posterior cingulate cortex (PCC), and precentral/postcentral gyrus. Random-effect model was used across subjects, and multiple comparisons were corrected at cluster level using Gaussian random field theory (Z>2.3, cluster significance: $p<0.05$ corrected).

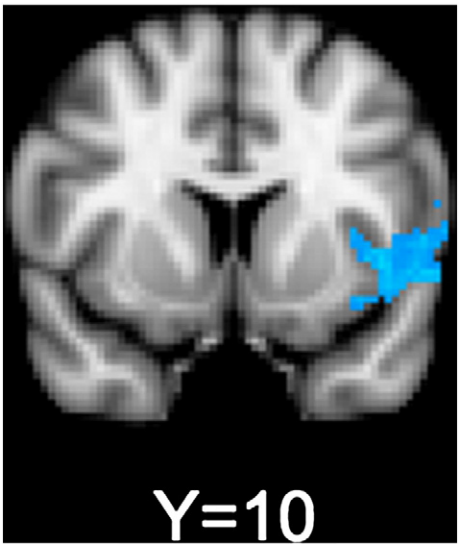

Fig. 3. The contrast of trials where the LL alternative was selected minus trials where the SS alternative was selected was associated with individual variability in stochasticity. More stochastic decision makers recruited more LL choice-related activity in the left insula and inferior frontal gyrus (IFG). Random-effect model was used for this group-level analysis, and multiple comparisons were corrected at cluster level using Gaussian random field theory ($Z>2.3$, cluster significance: $p<0.05$ corrected).

a peak at (−30, 34, 40, MNI) which was within our observed cluster for the LL–SS contrast. In another study, which included an adaptive discounting procedure but did not include a value regressor, Wittmann et al. (2007) reported an association between LL choice and a cluster within the left posterior insula with a peak at (−40, −6, 7, Talairach space), which also was within our significant main effect cluster map (though unlike their study, we did not observe corresponding significant activation in the right hemisphere). More recently, in a study with an alternative method of tailoring intertemporal choices to individual discounting, Christakou et al. (2011) also reported LL choice-related activation in the left IFG in BA 9 as well as in the left dlPFC BA 6, although in neither case did the reported peak voxels of these clusters fall within the clusters reported here.

Evidence outside the neuroimaging literature provides preliminary support for a causal association between the activity of the dlPFC and LL preference. In a recent Transcranial Magnetic Simulation (TMS) study on delay discounting, Figner et al. (2010) observed reduced preference for LL alternatives when functioning of the left dlPFC was temporarily disrupted. In another relevant study (Cho et al., 2010), where continuous Theta Burst Stimulation (cTBS) was applied to excite dlPFC, the discounting rate was reduced compared to that during a sham condition. Also of interest, Hare et al.(2009) reported that MR signal change in the left dlPFC indirectly mediated activation in the vmPFC (a region which tracks goal value at the time of decision-making) while participants were exercising self-control (forgoing liked-but-unhealthy food items). Similarly, dlPFC activity was increased when smokers were thinking about long-term consequences of smoking to reduce craving evoked by cigarette cues (Kober et al., 2010).

Although, as discussed above, we cannot rule out that the reported association between LL choice and vmPFC activity is related to residual value, it is worth noting that this region has been associated in prior studies with valuation of and preference for future rewards (Ballard and Knutson, 2009; Christakou et al., 2011; Sellitto et al., 2010), as well as value-tracking in other contexts (Hare et al., 2008; Levy et al., 2010; Plassmann et al., 2007). With regard to ACC, a recent fMRI study (Peters and Büchel, 2010) also suggested a controlling function of ACC during intertemporal decision-making that interacts with neural correlates of episodic imagery (in particular the hippocampus).

Moderators of prefrontal association with LL choice

Steeper temporal discounters demonstrated greater LL vs. SS signal differential in the left dlPFC, PCC, and precentral/postcentral gyrus. All these clusters, however, fell outside the overall LL>SS contrast map, so there is reason for caution with regard to interpreting these findings. One possibility is that the true relationship between choice and signal change in these regions is opposite in sign for low vs. high discounters (leading to an absence of a main effect of choice). Alternatively, and perhaps more plausibly, the absence of a main effect in these regions could be Type 2 error (a possibility that is bolstered with regard to the dlPFC based on the overlap between the uncorrected main effect and correlation maps (Supplementary Fig. 3)). But the converse is also possible, which is that some or all of the k^* correlational findings are spurious (Type 1 error). Therefore, we think interpretation of these findings as moderators warrants particular caution given the absence of overlap with main effect clusters. That said, if the LL association in the dlPFC is related to cognitive control demands, then the data in turn suggest that cognitive control is less relevant to choice among participants that are more patient. This is perhaps surprising; one might hypothesize the opposite — that individuals exhibiting more patience would evidence the greatest prefrontal activation associated with LL choice, since these individuals were presented with larger SS alternatives. However, the present finding is consistent with the findings reviewed in the introduction. Most directly relevant, cigarette smokers (who, as a group, tend to discount steeply) exhibit hyper-restraint in their intertemporal choices. Perhaps individuals with more extreme underlying impatience orient to intertemporal monetary choices as situations in which restraint should be deployed. By contrast, for an individual with little underlying impatience for money, intertemporal monetary choices may seem a matter of mere preference rather than as a self-control challenge.

The degree of stochasticity in individuals' intertemporal choices moderated LL-related brain activity within the left insula and IFG, and corrected cluster maps for the correlation and main effect included substantial overlap. The insula has been reported in response inhibition studies (Garavan et al., 1999; Wager et al., 2005), and it may carry affective signals critical in linking motivation to action selection (Wager and Barrett, 2004). An alternative speculation regarding the functional significance of the insula finding is that it may be related to ambivalence participants experienced while making difficult intertemporal choices. Data we previously reported (Luo et al., 2009; Luo et al., 2011) suggest decision makers choose LL on some occasions even though the SS recruits more value-related signal when the alternatives are encountered individually. Perhaps for this reason, LL selections may tend to be associated with greater ambivalence, and this may be especially true for participants that are less rule-governed in their approach to the task. As noted above, posterior insula has previously been associated with LL choice (Wittmann et al., 2007). Both risky choice (Paulus et al., 2003) and directly aversive states including pain are associated with activation in this region (Singer et al., 2004). It is worth noting that the insula was robustly associated with slower RT (a plausible marker of ambivalence) during decision-making (see Supplementary Fig. 1).

Although we know of no work that has looked at the clinical or social relevance of individual variation in stochasticity of intertemporal choice, there are natural predictions that could be made. In domains in which success demands consistent farsightedness (e.g. maintenance of reputation, moderation in spending behavior, success in smoking cessation), greater stochasticity would be predicted to be associated with poor outcomes, explaining variance incremental to that explained by overall discounting. Conversely, in domains in which success depends on only occasional farsightedness (e.g., getting a vaccination or availing oneself of commitment devices such as

automatic savings plan), greater stochasticity would be predicted to be associated with better outcomes.

Limitations of the study

Our modeling approach can fairly be characterized as heavy-handed. We assumed a simple hyperbolic function for discounting, and implicitly, we also assumed that the utility function for participants is linear. With regard to hyperbolic discounting, however, this assumption does not have significant potential implications with regard to estimates of individual levels of discounting given that we used a single delay during all choice trials. Our hyperbolic model does entail that our measure of stochasticity is conditioned on choice being a function of the *ratio* of the SS and LL. If, for example, a participant cared instead only about the absolute difference in reward size (e.g., chose the LL if and only if it was $10 or more greater than the SS), then that participant's estimated stochasticity would be inflated. The problem is reduced by the fact that separate models were constructed within two relatively narrow LL reward ranges (53 ± 7 and 28 ± 7). Moreover, the association between the *predicted* and *observed* inconsistency of responses to those alternative pairs that were repeated during test sessions provides assurance that at the group level, estimation of stochasticity is not solely a function of mis-modeling. But it remains possible that stochasticity estimates are confounded with the appropriateness of the modeling assumption used (indeed this is certainly the case to some degree).

Finally, the discount model we used ignores diminishing marginal utility. We have assumed that the individual variation in intertemporal choice trade-offs reflect differences in discounting, but they could as well reflect differences in the utility function. An individual unwilling to wait four months for an amount twice that of an available SS may do so because he discounts steeply. Alternatively, he may discount modestly, but exhibits steep diminishing marginal utility such that the utility of the larger amount is only slightly larger than that of the smaller (Ho et al., 1999; Pine et al., 2009; Pine et al., 2010). Both of these interpretations should be kept in mind as these data do not allow them to be disentangled. We note though, that while procedures do exist for disentangling (Andersen et al., 2008), it is not clear whether diminishing marginal utility is not itself related to delay discounting (Jevons, 1879). One reason that $(2X) may not be treated as twice as valuable as $X is that the second $X will tend to impact the stream of consumption later in time.

Conclusions

At the group level, findings from this correlational study are consistent with the conception of LL choice as associated with greater prefrontal recruitment. However, the findings suggest a divergence from what is typically observed among executive function tasks. For executive function tasks such as the Stop-Signal Task and the Continuous Performance Task, when parameters are individualized to make the "controlled" response challenging for each participant, prefrontal activation is typically greater among those exhibiting greater overall control (Aron and Poldrack, 2006). This is in contrast to the pattern we observed in the present study, in which participants that made more consistent and more farsighted choices exhibited *less* prefrontal recruitment during those choices. The pattern of moderation influence on prefrontal task-related activity suggests that LL choice robustly engages executive control only among a subset of individuals.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2011.08.004.

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