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Separate and overlapping brain areas encode subjective value during delay and effort discounting

Stijn A.A. Massar [a,1], Camilo Libedinsky [a,b,1], Chee Weiyan [a], Scott A. Huettel [c], Michael W.L. Chee [a,*]

[a] Center for Cognitive Neuroscience, Neuroscience & Biobehavioral Disorders Program, Duke-NUS Medical School, Singapore
[b] Department of Psychology, National University of Singapore, Singapore
[c] Department of Psychology and Neuroscience, Duke University, Durham, NC, USA

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ABSTRACT

Making decisions about rewards that involve delay or effort requires the integration of value and cost information. The brain areas recruited in this integration have been well characterized for delay discounting. However only a few studies have investigated how effort costs are integrated into value signals to eventually determine choice. In contrast to previous studies that have evaluated fMRI signals related to physical effort, we used a task that focused on cognitive effort. Participants discounted the value of delayed and effortful rewards. The value of cognitively effortful rewards was represented in the anterior portion of the inferior frontal gyrus and dorsolateral prefrontal cortex. Additionally, the value of the chosen option was encoded in the anterior cingulate cortex, caudate, and cerebellum. While most brain regions showed no significant dissociation between effort discounting and delay discounting, the ACC was significantly more activated in effort compared to delay discounting tasks. Finally, overlapping regions within the right orbitofrontal cortex and lateral temporal and parietal cortices encoded the value of the chosen option during both delay and effort discounting tasks. These results indicate that encoding of rewards discounted by cognitive effort and delay involves partially dissociable brain areas, but a common representation of chosen value is present in the orbitofrontal, temporal and parietal cortices.

Introduction

Deciding whether to pursue a reward involves weighing its value against the cost involved in its acquisition. The computation of the integrated value of a reward with its associated cost in the brain (subjective value) is thought to be critical in guiding choice behavior (Kable and Glimcher, 2009; Rangel et al., 2008). One cost that is often incurred when obtaining a reward is the delay that one has to endure before receiving it. Having to wait for a reward decreases the preference for such an option. Accordingly the value of delayed rewards is discounted along a hyperbolic discounting curve (Ainslie, 1975). Neuroimaging studies have identified a network of brain areas – the ventromedial prefrontal cortex (vmPFC), ventral striatum (vSTR), posterior cingulate cortex (PCC) and lateral parietal cortex – that are engaged during decisions that involve delayed rewards (delay discounting; Bickel et al., 2009; McClure et al., 2004; Pine et al., 2010; Weber and Huettel, 2008; Wittmann and Paulus, 2009), showing activation that correlates with the subjective value of delayed rewards (Kable and Glimcher, 2007; Peters and Büchel, 2009; Pine et al., 2009).

Similar to delay, the effort involved in obtaining a reward can be considered a cost that may influence preference. Behavioral studies have shown that rewards that entail higher effort are chosen less often compared to those requiring little effort (Treadway et al., 2009), and their values are discounted accordingly (Kool and Botvinick, 2014; Westbrook et al., 2013). The concept of effort discounting has strong clinical relevance. Excessive discounting of effortful rewards for instance has been associated with clinical symptoms such as apathy and anhedonia in major depressive disorder (Bonnelle et al., 2014; Treadway and Zald, 2013) and schizophrenia (Fervaha et al., 2013; Gold et al., 2013). Moreover, a long-term imbalance between the perceived amount of effort invested and the received rewards may lead to negative health outcomes such as burnout and cardiovascular disease which makes effort discounting an important topic of research (Bakker et al., 2000; Siegrist, 2010).

The majority of neuroimaging studies on effort discounting have focused on physical effort, since this type of effort is easily quantified and is readily translatable across species. However, many human activities (e.g., most office jobs) require a high degree of cognitive effort (Hunt and Madhyastha, 2012), and in many daily life decisions the critical cost is cognitive effort (e.g., choosing to study more for an

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[*] Corresponding author at: Center for Cognitive Neuroscience, Duke-NUS Medical School, 8 College Rd, #06-18, Singapore 169857, Singapore. Fax: +65 6221 862.
E-mail address: michael.chee@duke-nus.edu.sg (M.W.L. Chee).

[1] These authors have contributed equally.

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exam to achieve a higher score). Laboratory studies have demonstrated that people tend to avoid tasks that are cognitively effortful, and discount the value of associated rewards (Kool and Botvinick, 2014; Kool et al., 2010; Mcguire, 2011; Westbrook, et al., 2013). Importantly, monitoring the level of effort in cognitive tasks may not be supported by the same brain areas as monitoring effort in physical tasks (motor areas, ACC, and anterior insula for physical tasks versus lateral frontal cortex and ACC in cognitive tasks; Jansma et al., 2007; Mcguire and Botvinick, 2010; Prevost et al., 2010; Schmidt et al., 2012).

So far only two studies have examined the neural integration of cognitive effort costs and reward value in the context of decision-making. Botvinick et al. (2009) found that rewards that followed high cognitive effort elicited a blunted ventral striatum response compared to rewards associated with low effort (Botvinick et al., 2009). Moreover, the attenuation of reward responses correlated with the dlPFC activity during the effortful task (reanalysis of the original data in Kool et al., 2013). Schmidt et al. (2012) provided concurring support for the engagement of dlPFC and vSTR in effort and reward monitoring respectively. Moreover, greater connectivity between ventral striatum and the caudate was observed during the execution of the effortful task. While these studies evaluated brain activity during task execution and receipt of reward, it remains unclear how subjective value computations are represented during decisions about cognitive effort.

The primary aim of the present study was to explore the neural substrates underlying cognitive effort discounting during the period when decisions are made. We compared the neural substrates of effort discounting with those of delay discounting to additionally examine the extent to which both types of discounting recruit separate or shared brain structures. Subjects made choices between rewards that were contingent on different levels of effort or delay while undergoing fMRI. There is reason to expect that effort discounting would involve separable brain regions from those recruited by delay discounting. Animal studies and human neuroimaging studies have demonstrated that different types of cost discounting (including delay discounting and physical effort discounting) are supported by different neural structures, and their subjective values are represented in non-overlapping brain areas (including the anterior cingulate and anterior insular cortices for effort; Burke et al., 2013; Peters and Büchel, 2009; Prevost, et al., 2010; Rudebeck et al., 2006). A similar dissociation could be present for delay and cognitive effort discounting. The costs of effort and delay were calibrated to minimize the differences in their respective subjective values and to increase the comparability of both domains.

Methods

Participants

Twenty-three healthy adults participated in the study (12 females, mean age = 22.2 years, SD = 2.5 years). All participants provided informed consent, in compliance with the requirements of the National University of Singapore Institutional Review Board. Participants were selected from a pool of university students who responded to a web-based questionnaire. They had to be right-handed, be between 18 and 30 years of age, not be on any long-term medication, and have no history of any psychiatric or neurologic disorders. All participants indicated that they did not smoke, or consume any medications, stimulants, caffeine, or alcohol for at least 24 h prior to scanning.

Experimental design

During an initial session, participants were screened to make sure they showed sufficient delay discounting (discount index < 0.9 in delay discounting calibration task; see below). Eligible participants were invited for an fMRI session approximately one week later. During this session they first familiarized themselves with the effort by performing the effort task (described below), after which they performed three out-of-scanner calibration tasks. Subsequently, they were placed inside the scanner and performed the in-scanner delay discounting (DD) and effort discounting (ED) tasks. Because participants took part in a larger study in which test–retest reliability of the discounting task and the effects of sleep deprivation on discounting behavior were examined (reported elsewhere, Libedinsky et al., 2013), they were only compensated two months after the scanning session. The compensation was determined in a separate session and was based on the choices made during the scanner session.

Effort task

Effort was introduced by requiring participants to type backwards a specified number of words. This task required overriding a prepotent, well-practiced response (reading and typing the word in normal order) and planning a novel sequence of actions (reversing the letter strings). These processes can be considered as aspects of cognitive control (Norman and Shallice, 1986). Although there are clear physical aspects to this task (e.g., executing the key strokes), those aspects are secondary compared to the cognitive challenges introduced by the task. An advantage of this task is that by varying the number of words, the level of effort can be parametrically scaled to individually match the subjective costs of different delay durations. Participants familiarized themselves with this type of effort by typing 50 words backwards before starting the calibration tasks.

Out-of-scanner calibration tasks

Three out-of-scanner calibration tasks were performed: *delay*, *effort*, and *effort/delay*. The calibration tasks enabled us to determine the indifference points (i.e., the amount of money that the subject considered equivalent to a large reward of $20 at a given level of costs [delay or effort]). A calibration was performed for delay discounting, providing the indifference points at increasing delays of 2, 3, 4, 5, and 6 months. A separate calibration was performed for effort discounting, providing the indifference points at five increasing effort levels (increasing number of words). Crucially, before commencing this effort discounting calibration, an effort/delay calibration task was performed to titrate the numbers of words (effort levels) for each individual. This procedure returned the number of words that participants considered as equivalent in cost to the delays that were used in the delay discounting task. All calibration tasks followed a similar binary search algorithm (adapted from Weber and Huettel, 2008). Participants performed two runs of each calibration task in approximately 15 min before starting the scanner tasks.

Delay discounting calibration

Participants were shown pairs of monetary offers that would be available at different delays (Fig. 1A). One option, the larger later option (LL), offered a high amount of money ($20), at a longer delay (3, 4, 5 or 6 months). The other option (smaller sooner option, or SS) offered a smaller amount (variable), at the earliest possible time (2 months). We included a control condition in which both LL and SS were delayed by 2 months. The magnitude of the LL options was always $20. The magnitude of the SS option was adjusted on a trial-by-trial basis. On the first trial it was set as a random amount between $7 and $12. On subsequent trials the SS amount was varied based on the subject's choices (i.e., increased if the LL was chosen, decreased if the SS option was chosen). This adjustment procedure was iterated for six trials per delay, after which the indifference point was determined as the average of the largest amount for which the subject chose the SS option and the smallest amount for which the subject chose the LL option.[2] The indifference point reflects the amount that the subject perceived as neither better nor worse than \$20 at the given delay (see Fig. 1B).

Effort/delay calibration

To determine the effort level (number of words) that the subject found equally costly at a given delay, offer pairs were constructed in which one option offered \$20 at one of the five delays, and the other option offered \$20 at the earliest time, but required typing a specified number of words. The number of words was adjusted based on the subject's choices (i.e., increased if the effortful option was chosen, decreased if the delayed option was chosen). After six trials for each delay, the number of words valued equivalently to the given delay was determined.

Effort discounting calibration

Using the numbers of words provided by the effort/delay calibration, offer pairs were constructed such that the subject had to choose between options that differed by the level of effort required. The larger harder option (LH), offered a high reward (\$20) at a given level of effort (number of words). The smaller easier option (SE) did not require typing words, but offered a smaller amount of money. Similar to the delay discounting calibration, SE offers were adjusted based on the subjects' choices, and indifference points were determined after six trials of each effort level (see Fig. 1A). All calibration tasks were performed twice and the indifference points extracted from the second runs were used to construct the offers for the in-scanner discounting tasks.

Scanner tasks

As with the calibration tasks, the scanner task consisted of choices between a larger, more costly reward, and a smaller, less costly reward (LL and SS for delay discounting; LH and SE for effort discounting). The amount for the costly options was fixed at \$20, while the cost levels were varied per trial (2–6 months for delay discounting trials and the equivalent number of words for effort trials). The amounts offered for the non-costly options (SS or SE) were varied on every trial. For 15 trials this amount was set to be high (\$19–\$20), on 15 trials this amount was low (\$3–\$7), on the remaining 30 trials the offer was varied (±\$1) around the calibrated indifference point corresponding to the delay or effort level that was presented for the costly option. This manipulation allowed the optimization of indifference points in the scanner setting, such that subjects chose the alternative option on approximately half of the trials. Participants performed 3 runs of the delay discounting task and 3 runs of the effort discounting task in alternating order, each consisting of 60 trials.

Compensation

Participants were compensated in a separate session two months after the scanning session. Pay-out was determined by randomly drawing three trials from choices made during the scanner session (from both the scanner and the calibration tasks). If a trial was drawn that involved a choice for a SS option or a SE option, the indicated amount was sent to them as an Amazon.com gift voucher via email that same day. Note that the shortest possible delay of two months had already passed at that point in time. On the other hand, if one of the drawn trials involved a longer delay (LL), the reward for that trial was emailed to them as an Amazon.com voucher at the indicated delayed date. If one of the drawn choices involved an effort trial in which the effortful option (LH) was chosen, the participant was required to type out the indicated number of words in exchange for the chosen reward. In order to control for any extra delay involved in typing out words, the reimbursement session had a fixed duration of 30 min for all participants. During this time they had to type the indicated number of words, or had to sit in and wait (in case a no effort choice was drawn) until the end of the session, before the reimbursement was sent to them.

Behavioral data analysis

Behavioral data was analyzed using MATLAB (MathWorks, Natick, USA). The discounting curves for delay and effort discounting were constructed by connecting the indifference points for each month/number of words. The area under these discounting curves (AUC) determined the discount index (discount index; Fig. 1C) thus providing theory-independent estimates of delay and effort preferences (Myerson et al., 2001). The discount index ranged from 0 (high discounting) to 1 (no discounting). Seven out of all screened subjects did not show sufficient discounting during the screening session (discount index > .9), and were not included in the scanner session. For participants who entered the fMRI session discounting indices ranged from .43 to .81 (mean = .65, s.d. = .10) during screening.

fMRI data acquisition and analysis

Imaging was performed on a 3-T Siemens Tim Trio scanner (Siemens, Erlangen, Germany) fitted with a 12-channel head coil. Functional images were collected using a gradient echo-planar imaging sequence (TR: 1500 ms; TE: 20 ms; flip angle: 90°; field-of-view: 192 mm × 192 mm; matrix size: 64 × 64). We acquired 34 oblique axial slices (4 mm thick with no inter-slice gap) parallel to the inter-commissural plane. A high-resolution 3D-MEMPRAGE (Multi-Echo Magnetization-Prepared Rapid-Acquisition Gradient Echo) sequence was obtained so that anatomical images could be normalized into common stereotactic space.

The MRI data were analyzed using BrainVoyager QX 2.3.0.1750 (Brain Innovation, Maastricht, The Netherlands) and MATLAB (MathWorks, Natick, USA). Inter-slice timing differences within each functional acquisition were corrected using cubic spline interpolation. Intra-session image alignment to correct for motion was performed using the first image of the first functional run as the reference image. Spatial filtering employed a Gaussian filtering kernel with an 8 mm FWHM for group level activation maps. Linear trend removal and a high-pass filter of 160 s were applied. Functional volumes were registered to the high-resolution 3D anatomical image. Finally, all images were normalized to Talairach space.

Statistical analysis

To identify brain areas that encoded the subjective value of the delayed and effortful options (for DD and ED trials respectively), we used a general linear model (GLM) that contained six regressors. For each type of trial (DD or ED) the choice period was modeled with separate regressors for the mean signal and parametric regressors for the subjective value of the discounted options (delayed: LL or effortful: LH; which were the regressors of interest). Subjective value (SV) of the discounted options was derived from the pre-scanner calibration tasks (the indifference point for the given delay/effort level). These regressors were modeled across both near-indifference and far-from-indifference trials. In order to control for any contributions of the non-discounted option the SVs of these options were modeled separately, and the regressors for discounted value were orthogonalized with respect to these non-discounted regressors. Furthermore, RT was incorporated into a parametric regressor of non-interest, for DD trials and ED trials separately. Each of the regressors was modeled as a 4-s boxcar function, convolved with a canonical HRF function, starting at trial onset. In order to examine to what extent results from the main GLM could be explained by the cost level rather than subjective value, a control GLM

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[2] If the SS option was chosen consistently throughout all six iterations, the indifference point was set to the average between the last offered (lowest) amount and zero. If only LL options were chosen, the indifference point was set to the average between the last offered (highest) amount and \$20.

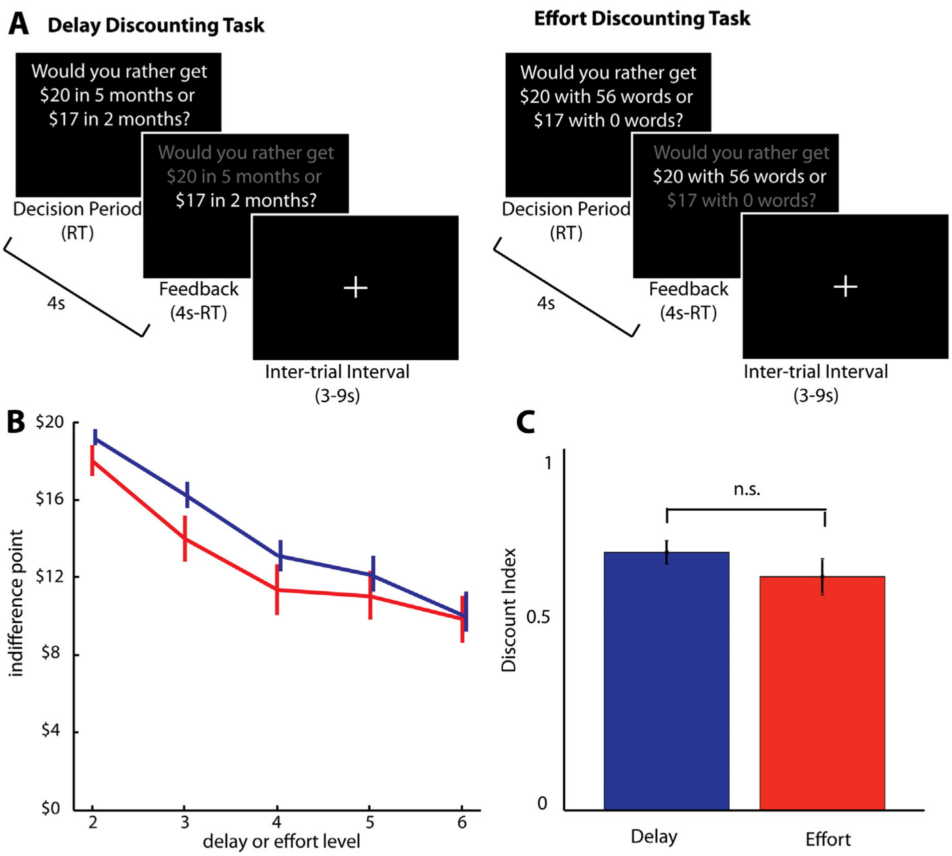

Fig. 1. A) Trial sequence in the delay discounting (left) and effort discounting (right) tasks. B) Calibrated indifference points for the different levels of delay (blue line) and effort (red line). Delay levels refer to the number of months (2–6), and effort levels refer to individually calibrated numbers of words that were considered to be equally costly as the levels of delay. C) Discount index derived from the delay and effort discounting curves.

was performed which was identical to the main GLM but the SV regressor was replaced by a cost regressor (level of delay or level of effort; see Supplementary Information).

Additionally, a GLM was performed in which the subjective value of the chosen option was modeled. This GLM included six regressors that represented DD and ED trials separately: the mean signal during choice period, the subjective value of the chosen option, the subjective value of the unchosen option, and reaction time (RT). Subjective values were determined as the calibrated indifference point if the discounted option was chosen (LL or LH), or the smaller amount offered for the non-discounted option (SS or SE) if that option was chosen. The regressors for the chosen value were orthogonalized with respect to the unchosen value regressors. As in GLM1, all regressors were modeled as 4-s boxcar functions, starting at trial onset, and intertrial interval (ITI) was modeled as baseline. In both GLMs trials in which no response was given (misses) were modeled separately as a nuisance regressor.

Results

Behavioral results

Out-of-scanner calibration tasks

The indifference points derived from the calibration tasks were used to construct discounting curves (Fig. 1B). A repeated measures ANOVA indicated that reward value was discounted with increasing cost levels (cost level main effect; $F(4, 88) = 49.59$, $p < .001$), with no difference between delay and effort discounting (domain main effect: $F(1, 22) = 1.38$, $p = .25$) nor a domain × cost level interaction ($F(4, 88) = .71$, $p = .53$). Analysis of the area under these discounting curves (discount index) similarly, showed no significant difference between delay discounting and effort discounting ($t(22) = 1.3$, $p = .21$, Fig. 1C).

In-scanner behavior

To verify the validity of the calibration procedure, discounting curves for the in-scanner task were calculated in the same manner. Fig. 2 shows that in the in-scanner task subjects indeed discounted rewards that came at higher costs (cost level main effect: $F(4,88) = 30.34$, $p < .001$). During the in-scanner task however, a difference between the SVs for delay and effort discounting emerged (domain main effect: $F(1, 22) = 4.83$, $p = .039$; with no domain × cost level interaction ($F(4,88) = .44$, $p = .78$)). The domain main effect indicated that SVs for delayed rewards were slightly higher than those for effortful rewards. Discount indices showed a borderline effect in the same direction ($t(22) = 1.91$, $p = .069$). Despite this overall difference the in-scanner discount index for effort and delay discounting were positively correlated ($r = .53$, $p < .01$; Fig. 2A; inset 2), showing that across subjects there was a strong concordance between SVs for effort and delayed options. Furthermore, in-scanner discount indices were strongly correlated with those during calibration (delay: $r = .83$, $p < .001$; effort: $r = .72$, $p < .001$; see Fig. 2B & C). In more detail, analyzing the in-scanner choices as a function of SV difference between both options showed that the proportion of costly choices was lowest when the associated discounted SV was lower, intermediate when SV was similar, and highest when the discounted SV was higher than the value of the corresponding non-costly option. This pattern was true for both delay and effort discounting ($F(1,22) = 165.78$, $p < .001$; Fig. 2D). Reaction times showed an inverted-U shaped pattern, being longer for trials in which both options had similar SVs, and faster when SVs were dissimilar ($F(1,22) = 30.85$, $p < .001$; Fig. 2E). Overall, costly choices

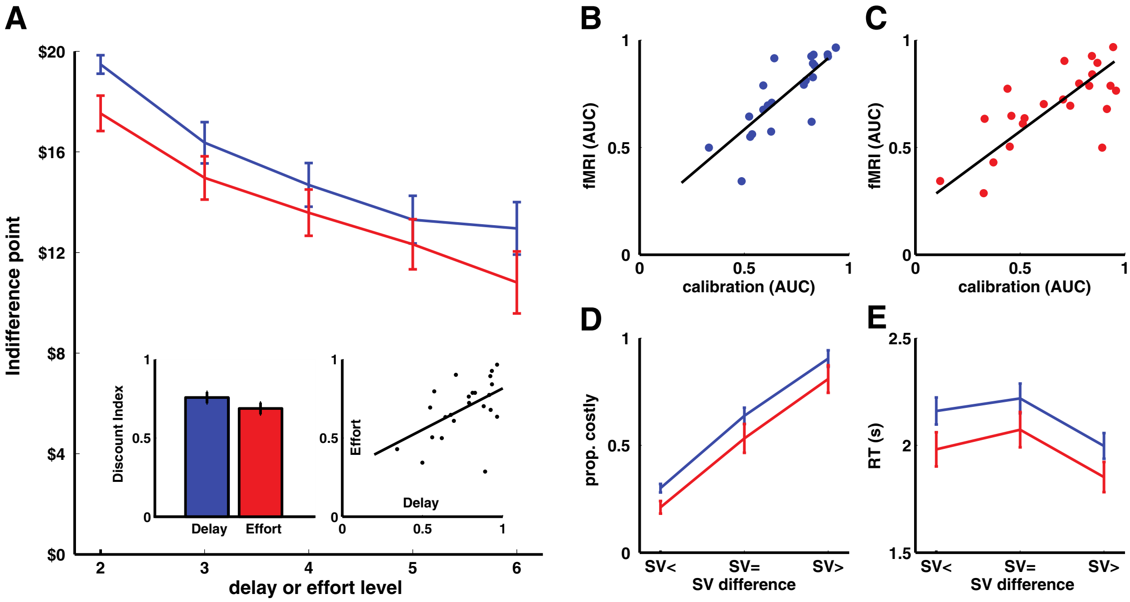

Fig. 2. In-scanner behavior for delay (blue) and effort discounting (red). A) Mean indifference points for consecutive cost levels (delay: months; effort: equivalent number of words), mean discount indices (AUC; in inset 1) and correlation between effort and delay discount index (inset 2). B) and C) correlations between discount indices during calibration and during fMRI runs. D) and E) proportion of costly choices and RTs for trials in which the SV for the costly option is lower (SV<), similar (SV=), or higher (SV>) than the non-costly option. Error bars represent SEM.

and RTs were slightly lower during effort discounting than during delay discounting (choice: $F(2,44) = 7.12$, $p < .05$; RT: $F(1,22) = 35.95$, $p < .001$).

fMRI results

Subjective value of delayed/effortful option

During DD trials, the subjective value of the delayed option correlated with activity in a network of regions, including the dorsal and ventral regions of the medial prefrontal cortex (dmPFC and vmPFC), the posterior cingulate cortex (PCC) and bilateral posterior parietal cortex (Fig. 3; Table 1). These regions are consistent with the neural substrates commonly indicated in delay discounting (for reviews see Carter et al., 2010; Luhmann, 2009; Peters and Büchel, 2011). Control analysis showed that the dmPFC and parietal activations could be explained by cost level alone (delay level), but vmPFC and PCC activations were only explained by subjective value (Supplementary Fig. 3).

During ED trials, the subjective value of the effortful option correlated with activity in the left temporal and bilateral parietal

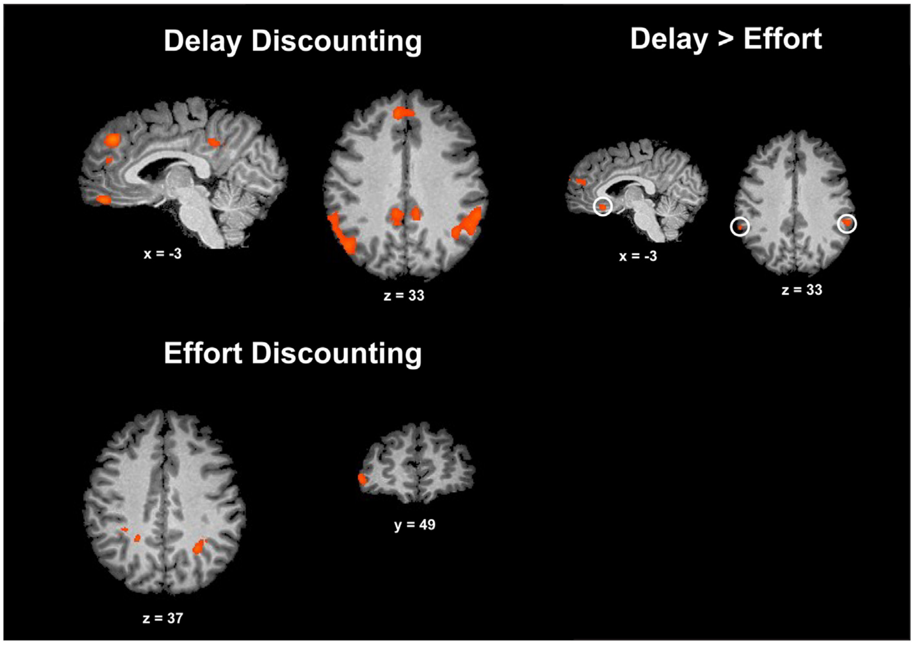

Fig. 3. Areas in which activation correlated with subjective value of delayed and effortful options (threshold: $p < 0.001$ voxel-level, and $p < 0.05$ cluster level for all activations except for delay > effort contrast in sagittal plain, where $p < 0.005$ voxel-level, and $p < 0.05$ cluster level was applied).

Table 1
Regions that correlate with the subjective values of the discounted option orthogonalized with respect to non-discounted value.

Anatomical description	BA	Cluster size	Peak location (Talairach)			t-value
			x	y	z	
Delay discounting						
R middle temporal gyrus	21	2823	56	−20	−9	5.92
L medial frontal gyrus	8	2006	−7	40	36	5.66
R middle frontal gyrus	47	2458	41	37	−3	5.58
L superior temporal gyrus	38	246	−34	7	−24	5.54
L superior temporal gyrus	22	2924	−49	−23	−9	5.49
R precuneus	19	5071	41	−68	42	5.47
R middle frontal gyrus	6	605	26	13	54	5.39
L supramarginal gyrus	40	5604	−52	−50	18	5.33
L medial frontal gyrus	11	1271	−1	46	−12	5.27
L inferior frontal gyrus	47	213	−31	22	−6	5.24
R inferior frontal gyrus	45	960	47	19	15	5.11
R middle frontal gyrus	6	783	35	1	39	5.03
L middle frontal gyrus	6	209	−43	7	51	4.81
R superior frontal gyrus	6	349	14	28	54	4.77
R medial frontal gyrus	10	183	14	58	3	4.63
L cingulate gyrus	31	450	−7	−41	33	4.60
R cingulate gyrus	31	390	8	−41	33	4.55
R precuneus	7	181	11	−59	45	4.48
L superior frontal gyrus	6	153	−16	19	54	4.41
R anterior cingulate	32	185	8	43	12	4.35
R middle temporal gyrus	21	251	50	−47	3	4.17
Delay > effort						
L inferior parietal lobule	40	702	−59	−43	20	5.04
L inferior frontal gyrus	47	216	−35	14	−23	4.46
R inferior parietal lobule	40	243	58	−37	34	4.28
L inferior frontal gyrus	45	81	−51	29	7	3.99
L anterior cingulate[*]	32	162	−56	−13	22	3.97
L medial frontal gyrus[*]	9	621	−68	−24	22	3.72
Effort discounting						
R supramarginal gyrus	40	648	33	−49	31	4.79
L cingulate gyrus	31	81	−23	−46	34	4.60
L inferior temporal gyrus	37	270	−54	−37	−15	4.58
L inferior frontal gyrus	10	513	−42	50	−1	4.26
L inferior parietal lobule	40	81	−30	−40	40	4.20
L inferior parietal lobule	40	189	−41	−52	43	4.08
L postcentral gyrus	2	81	33	11	−18	−4.20
R superior temporal gyrus	38	108	−65	−22	22	−4.01

Clusters were obtained using a voxel-level threshold of $p < 0.001$ and underwent cluster correction at $p < 0.05$ ($k \geq 108$ mm^3 for delay discounting; $k \geq 81$ mm^3 for effort discounting).

[*] Voxel-level threshold of $p < 0.005$, cluster correction at $p < 0.05$.

cortex. Additionally, effortful SV was encoded in a left frontal cluster comprising the anterior portions of the dorsolateral PFC (dlPFC) and inferior frontal gyrus (Fig. 3; Table 1). Control GLM showed that the parietal but not the IFG activations could be explained by effort level rather than subjective value (Supplementary Fig. 3).

Direct Delay > Effort contrast revealed that activation in bilateral parietal cortex and left inferior frontal gyrus clusters was correlated more strongly with delayed value than with effortful value. The vmPFC and dmPFC clusters found earlier showed at a lower threshold ($p < .005$, voxel level threshold; $p < .05$ cluster level threshold). No regions showed significantly stronger coding for effortful value compared to delayed value (Effort > Delay contrast). There were no regions coding for both delayed and effortful value in a conjunction analysis.

Since behavioral reaction times were different for the delay discounting and the effort discounting tasks, we additionally analyzed the brain areas that correlated with the RT regressors. This analysis yielded an extensive thalamo-cortical network during both delay and effort discounting, but none of these areas showed significant differences between both tasks (Delay > Effort and Effort > Delay; see Supplementary Fig. 4).

Subjective value of chosen option

During DD trials activation correlated with chosen value in the right lateral orbitofrontal cortex (lOFC), dmPFC, posterior cingulate middle temporal gyrus and the supramarginal gyrus in the parietal lobe bilaterally (Fig. 4; Table 2). A direct Delay > Effort contrast showed that activation in the right supramarginal gyrus and superior temporal gyrus correlated more strongly with chosen value during DD as compared to ED trials. For ED, an extensive network of regions showed activation that correlated with chosen value, including a similar region in the lOFC. In addition, correlations were found in the anterior cingulate and posterior cingulate cortex, caudate nucleus, bilateral temporal and parietal cortex, and cerebellum (Fig. 4; Table 2). Activation in the ACC and left pre-central gyrus was correlated more strongly with chosen value during effort discounting as compared to delay discounting in an Effort > Delay contrast. Finally, a conjunction analysis revealed that overlapping areas in the precuneus, bilateral temporal cortex and the lOFC showed activation correlating with the chosen value during both DD and ED trials (Fig. 4; Table 2).

Discussion

This study set out to examine the neural correlates of value discounting by two types of cost, namely delay and cognitive effort. Results showed that decision making recruited large brain networks that were partially dissociable and partially overlapping for delayed and for effortful rewards. During delay discounting, a network including vmPFC, PCC, and lateral parietal cortex was activated in proportion to subjective value. This is in line with previous studies on delay discounting (Bickel, et al., 2009; Kable and Glimcher, 2007; McClure, et al., 2004; Peters and Büchel, 2009; Wittmann and Paulus, 2009). For choices including effortful rewards the subjective value of effortful options was encoded in the IFG, lPFC, and parietal cortex. In addition, choice value for effortful options was encoded in a network comprising the anterior and posterior cingulate cortex, caudate nuclei, cerebellum, bilateral temporal and parietal cortex and lateral OFC. Direct contrast revealed that the ACC activation was more strongly correlated in effort discounting relative to delay discounting. Finally, overlapping areas of temporal, parietal and lateral orbitofrontal cortex were involved in choice value representation during both delay and effort discounting.

A fronto-parietal network involved in cognitive effort discounting

A key finding of the current study was that several brain structures in frontal and parietal cortex encoded the subjective value of rewards discounted by cognitive effort. During the effort discounting task participants made choices, weighing monetary rewards against the effort (backwards typing of words) involved in obtaining them. This form of effort can be regarded as primarily cognitive, since backwards typing of words involves aspects of cognitive control (inhibiting the automated reading directions and the associated motor responses, and planning a novel, reverse sequence of actions).

A brain region that was found to be involved in the encoding of effortful choice value that may be of specific interest is the ACC. Previous studies on effort-based decision making have pointed to an important role for the ACC in the integration of effort and reward information in both humans (Kurniawan et al., 2010; Prevost, et al., 2010) and animals (Rudebeck, et al., 2006). Notably, these studies have focused on physical forms of effort. Interestingly, the ACC is also strongly engaged in cognitive control processes such as conflict monitoring and in reward/avoidance learning (Botvinick, 2007). It has recently been proposed that the ACC integrates the costs and benefits of cognitive control, by monitoring the required level of control, and weighing it against its associated value (Shenhav et al., 2013). Our results provide empirical support for this proposition by demonstrating that ACC activation

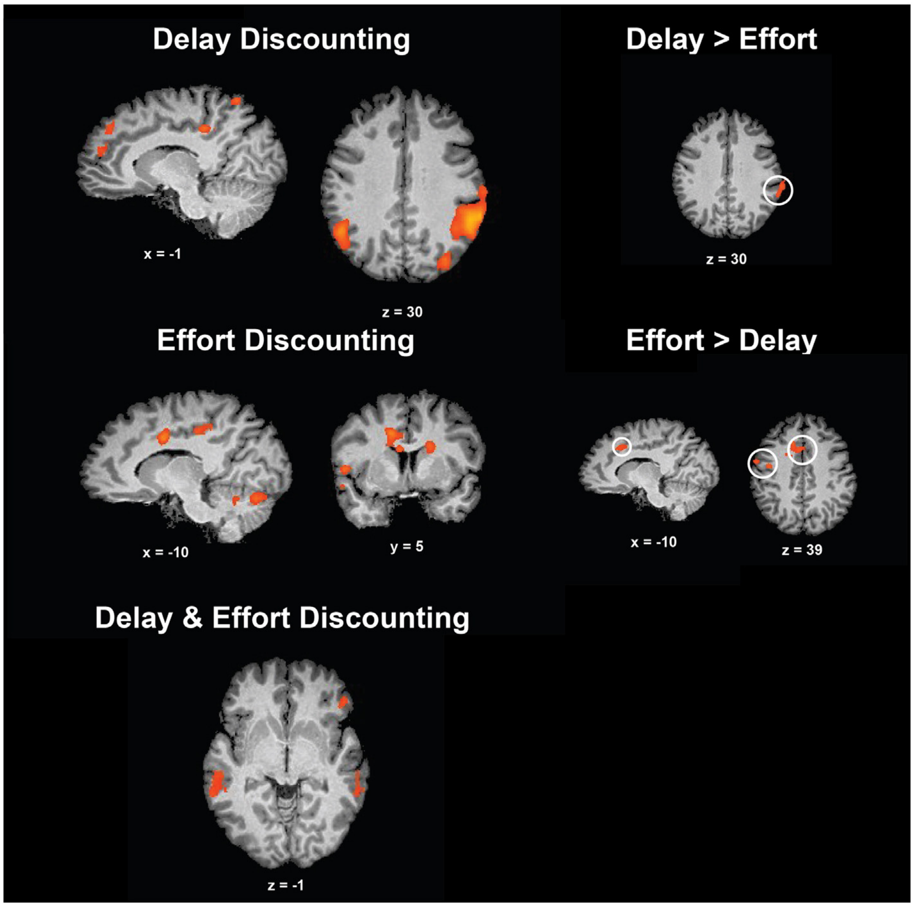

Fig. 4. Areas in which activation correlated with subjective value of the chosen option in delay trials, effort trials, the overlap, and delay > effort and effort > delay contrasts (threshold: $p < 0.001$ voxel-level, and $p < 0.05$ cluster level).

increased proportionally to choice value during decision making based on cognitive effort. Moreover, the current findings show that the encoding of choice value in the ACC was specific to effort-based but not intertemporal decision making.

Other brain areas that may be of interest are the lateral PFC areas that coded effortful value. The lateral PFC and IFG are implicated in aspects of cognitive control that may be relevant to the effort task in this study (e.g., overriding of prepotent responses, working memory manipulation; Bari and Robbins, 2013; Ridderinkhof et al., 2004), and in cognitive effort monitoring (Kool, et al., 2013; Mcguire, 2011). It should be noted however, that there was no evidence that the activation in the lateral PFC was uniquely related to effort discounting (as opposed to delay discounting). It is therefore possible that the lateral PFC activation found here is related to more general decision processes (e.g., exertion of self-control; Jimura et al., 2013; Kool, et al., 2013).

Effort discounting and delay discounting involve dissociable and shared brain areas

A second finding was that the network that encoded value during effort discounting in this study, was partially separated from the network involved in delay discounting task. Although a double dissociation was not found for all brain regions, several areas correlated more strongly with subjective value of delayed than effortful rewards (i.e., vmPFC, dmPFC and lateral parietal areas). On the other hand, the ACC was significantly more strongly correlated with choice value in effort discounting compared to delay discounting. This partial dissociation concurs with studies comparing delay discounting with physical forms of effort discounting in humans (Burke, et al., 2013; Prevost, et al., 2010), and animals (Rudebeck, et al., 2006), and suggests that during reward discounting, information about delay and effort costs is integrated with value information in at least partly different neural areas.

Such relative separation may seem somewhat at odds with the notion of a “common neural valuation system” (Montague and Berns, 2002). Different reward types (e.g., monetary, food or social rewards) are found to commonly activate a core network of brain areas, comprising most notably the ventral striatum and vmPFC (for reviews see: Bartra et al., 2013; Clithero and Rangel, 2014; Levy and Glimcher, 2012). In the same vein it could be expected that these core valuation regions would also commonly represent value during different types of cost discounting. There is little evidence, however, for such common valuation from studies that explicitly compared reward discounting by different types of cost (i.e., delay, probability, and physical effort; Burke, et al., 2013; Prevost, et al., 2010; Weber and Huettel, 2008, but see Peters and Büchel, 2009). One possible explanation for this may be that effort can be regarded as an action-related cost, whereas delay is considered a property of the reward outcome (Rangel and Hare, 2010). Studies have shown that value computations during action-based decisions are not necessarily supported by the vmPFC or ventral striatum, but rather by action specific brain areas (Wunderlich et al., 2009). Furthermore, lesion studies have demonstrated that the learning of action-value associations is specifically dependent on intact ACC (Camille et al., 2011; Rudebeck et al., 2008). Our data would concur with these findings showing a specific involvement of the vmPFC in delay discounting and the ACC in effort discounting.

In addition to the evidence for dissociable neural areas, several overlapping brain regions were found to code the value of the chosen option during both delay and effort discounting. These regions included the lateral OFC, bilateral temporal cortex and right inferior parietal lobule. Of relevance to the current study, overlapping value signals have been found in the OFC (albeit in more medial location) for decisions during delay and probability discounting (Peters and Büchel, 2009). Several studies that have examined chosen value in the context of value discounting have found very similar temporal parietal and frontal regions to code for chosen value of rewards discounted along various different costs (delay and probability; Hsu et al., 2005; Luhmann et al., 2008). The current study therefore suggests that delay and effort discounting are associated with value computations in both shared and dissociable brain areas.

Table 2
Regions that correlate with the subjective values of the chosen option orthogonalized with respect to unchosen value.

Anatomical description	BA	Cluster size	Peak location (Talairach)			t-value
			x	y	z	
Delay discounting						
R inferior frontal gyrus	47	3294	39	30	1	9.46
R supramarginal gyrus	40	18,549	52	−45	32	6.76
R superior parietal lobule	7	972	19	−61	59	6.59
R cingulate gyrus	31	540	4	−34	38	6.34
L supramarginal gyrus	40	3051	−50	−52	26	5.69
R precuneus	19	378	42	−85	40	5.65
L middle temporal gyrus	21	2106	−53	−24	−7	5.02
R middle frontal gyrus	6	513	25	20	52	4.91
R superior occipital gyrus	19	972	36	−76	26	4.89
L precuneus	19	324	−11	−88	46	4.76
L superior parietal lobule	7	810	−23	−58	58	4.62
R superior frontal gyrus	8	297	10	41	40	4.51
L superior frontal gyrus	10	567	−14	66	17	4.39
R middle temporal gyrus	19	135	49	−78	10	4.17
R precuneus	7	378	6	−54	37	4.1
L middle occipital gyrus	18	162	−17	−94	8	4.09
R superior frontal gyrus	9	189	12	50	22	4.08
Delay > effort discounting						
R supramarginal gyrus	40	945	63	−42	32	5.80
R middle temporal gyrus	39	162	56	−70	33	5.15
Effort discounting						
R caudate		3888	22	−24	26	6.65
R parahippocampal gyrus	36	4752	39	−28	−10	6.05
L cingulate gyrus	24	1350	−14	1	32	6.01
L middle temporal gyrus	21	2943	−59	−39	−3	5.92
L dentate nucleus		7776	−17	−53	−19	5.76
R precuneus	7	3753	4	−58	61	5.57
L superior frontal gyrus	10	567	−18	53	−2	5.35
L precentral gyrus	44	567	−53	8	5	5.19
R precuneus	7	891	15	−72	43	5.04
L inferior parietal lobule	40	648	−57	−37	37	4.89
R superior temporal gyrus	13	594	45	−45	25	4.87
R inferior frontal gyrus	46	540	46	38	4	4.81
R middle occipital gyrus	18	972	7	−94	16	4.76
L inferior temporal gyrus	20	378	−68	−22	−19	4.76
R cingulate gyrus	31	1026	12	−27	38	4.7
L claustrum		243	−33	−10	−8	4.68
L cingulate gyrus	24	162	−6	5	22	4.68
L superior temporal gyrus	22	432	−53	11	−8	4.63
R inferior parietal lobule	40	432	51	−36	35	4.57
L inferior temporal gyrus	37	567	−54	−55	−3	4.56
L middle temporal gyrus	21	432	−50	−19	−11	4.54
L cingulate gyrus	31	324	−10	−27	39	4.54
L lentiform nucleus		162	−18	−7	1	4.47
L middle occipital gyrus	18	1026	−24	−94	5	4.46
R culmen		243	34	−36	−25	4.43
L caudate		324	−18	−28	20	4.35
R precuneus	7	243	15	−57	45	4.3
R cingulate gyrus	24	270	4	−13	35	4.28
L tuber		324	−35	−82	−26	4.24
R lingual gyrus	18	189	6	−61	4	4.21
R declive		162	8	−70	−12	4.19
R middle frontal gyrus	47	243	33	38	−7	4.13
R uvula		162	18	−73	−23	4.13
Effort > delay discounting						
L cingulate gyrus	24	567	−2	−1	20	−5.48
L cingulate gyrus	32	1107	−12	18	35	−5.29
L precentral gyrus	6	243	−44	−7	37	−4.93
L precentral gyrus	6	189	−57	−1	40	−4.50
L inferior frontal gyrus	47	189	−59	20	−16	−4.37
Delay & effort discounting						
R superior temporal gyrus	13	486	45	−45	25	4.81
R middle temporal gyrus	21	1593	64	−28	−8	4.7
R inferior frontal gyrus	45	405	46	33	2	4.61
R inferior parietal lobule	40	432	51	−36	35	4.57
R superior temporal gyrus	13	486	−54	−27	−4	4.15

Clusters were obtained using a voxel-level threshold of $p < 0.001$ and underwent cluster correction at $p < 0.05$ ($k \geq 135$ mm^3 for delay discounting; $k \geq 162$ mm^3 for effort discounting; $k \geq 108$ mm^3 for conjunction).

Limitations

Although the current study provides evidence for the involvement of shared and separate neural correlates of delay and effort discounting, there are several limitations to the current study. Firstly, although the calibration tasks were designed to minimize differences in subjective values as discounted by delay or effort, the discounting curves did significantly diverge during the scanner task. Participants showed a slightly shifted preference while performing the scanner task, with slightly more costly choices for delay versus effort discounting. Such differences in subjective values may have contributed to findings of dissociable brain areas involved in effort and delay discounting. Despite this possibility, we believe that the calibration procedure helped to minimize any potential differences between effortful and delayed values, as was also evident from the positive correlation between the associated discounting indices. Consequently we would encourage the use of such methods in order to optimize the comparability of value scales, and to be able to quantify any divergence.

A second limitation is that during the decision phase of our task costly and non-costly options with varying subjective values were presented simultaneously. This may have made it more difficult to separately analyze the discounted value from non-discounted value. Additionally, the cue presentation period was not separated from the response period. In total, this makes it hard to analyze how the different value signals develop over time and to construct a detailed mechanistic model of effort-based decision. Any interpretations to that effect, therefore, warrant verification in future testing. This however, does not detract from the main findings that reveal the brain structures that encode subjective value during cognitive effort discounting.

Lastly the brain areas that were involved in cognitive effort discounting in the current study may not generalize to other cognitive tasks. Cognitive tasks may be considered effortful for different reasons (e.g., overriding automatic responses in Stroop tasks versus high monotony in sustained attention tasks), and may recruit different neural areas. Similarly, it could be possible that effort discounting based on different cognitive tasks may be represented in (partially) different brain areas. This presents an interesting possibility that could be addressed in future studies.

Conclusion

The present study demonstrated that reward value was discounted along increasing costs of both cognitive effort and temporal delay. The subjective value of rewards discounted by cognitive effort was represented in a fronto-parietal control network comprising IFG, lateral parietal and lateral prefrontal cortex. Delay discounting recruited a network that was partially dissociable from this effort network. Furthermore, chosen value was encoded in a network that was partly unique to effort discounting (ACC), and was partly overlapping with delay discounting in the lateral OFC, and the temporal and parietal cortices. Thus, while cost-based decision-making may incorporate cost-specific value information from partially separable brain regions, value may be coded in a shared network upon choice.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.06.080.

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