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

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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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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