Prefrontal cortex, cognitive control, and the registration of decision costs

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Human choice behavior takes account of internal decision costs: people show a tendency to avoid making decisions in ways that are computationally demanding and subjectively effortful. Here, we investigate neural processes underlying the registration of decision costs. We report two functional MRI experiments that implicate lateral prefrontal cortex (LPFC) in this function. In Experiment 1, LPFC activity correlated positively with a self-report measure of costs as this measure varied over blocks of simple decisions. In Experiment 2, LPFC activity also correlated with individual differences in effort-based choice, taking on higher levels in subjects with a strong tendency to avoid cognitively demanding decisions. These relationships persisted even when effects of reaction time and error were partialled out, linking LPFC activity to subjectively experienced costs and not merely to response accuracy or time on task. In contrast to LPFC, dorsomedial frontal cortex—an area widely implicated in performance monitoring—showed no relationship to decision costs independent of overt performance. Previous work has implicated LPFC in executive control. Our results thus imply that costs may be registered based on the degree to which control mechanisms are recruited during decision-making.

mental effort | functional MRI | task switching | avoidance | inferior frontal gyrus

Human choice behavior has been held to be subjectively rational, or, "rational, given the perceptual and evaluational premises of the subject (1)." One key subjective premise, according to influential rational accounts (2–4), is that intensive information processing can carry an internal cost. Accordingly, "better decisions—decisions closer to the optimum, as computed from the point of view of the experimenter/theorist—require increased cognitive and response effort which is disutilitarian (2)." On this view, decision-makers balance a motive to maximize gains with a motive to minimize decision costs. The concept of decision costs helps explain such behavioral phenomena as effort-accuracy tradeoffs (3, 5), reliance on fast and frugal heuristics (6), failure to consider all available alternatives (7), effort discounting (8), the use of stereotypes (9), and salutary effects of monetary incentives (10, 11). Amplified decision costs might play a role in clinical depression (12) and chronic fatigue syndrome (13). This idea is related to the view that decision-making consumes a limited resource (14), and, more generally, that humans act as cognitive misers (15).

The neural mechanisms that underlie the registration of decision costs have never been directly investigated. We hypothesized that costs might be evaluated based on the degree of engagement of brain regions subserving executive control; these specifically include lateral prefrontal cortex (LPFC) and dorsomedial frontal cortex (DMFC) (16–19). Our hypothesis finds support in existing evidence that decision makers prefer to minimize demands for working memory (20), task set configuration (21), and conflict resolution (22–24), all hallmark functions of the executive control system.

We focused our experiments on simple decisions: response selections in the context of a cued task-switching paradigm. Task switching is widely understood to demand executive control (25, 26); furthermore, previous work (27) and our own initial behavioral results (see below) suggest that participants prefer to minimize such demands. In two functional MRI (fMRI) studies, we tested whether

activity in executive control-related brain regions would account for internal decision costs (measured through participants' tendency to avoid a demanding task) even when external demands were controlled.

Decision costs can be documented in the laboratory by embedding decisions in a demand selection task (DST) (22, 28). Fig. 1 *A* and *B* illustrate a particular instantiation of the DST together with behavioral choice data. Participants ($n = 12$) were permitted to draw task trials repeatedly from either of two locations. Trials taken from one location demanded greater executive control by requiring participants to switch tasks more frequently (26). As expected, participants tended to avoid this high-demand location, instead drawing trials preferentially from the low-demand location.

The result of this preliminary experiment bolsters our hypothesis that activity in brain regions associated with control, such as LPFC and DMFC, might directly index the evaluation of internal decision costs. If this hypothesis is correct, activity in these regions should covary with internal costs even independently of external task conditions. We evaluated this possibility in two complementary fMRI experiments.

Experiment 1

Experiment 1 elicited repeated self-reports of experienced decision costs. Costs were measured in terms of participants' rated desire to avoid the task. Participants completed 10-trial blocks of simple decisions in a task-switching paradigm (judging the magnitude or parity of single digits). Participants were told that the specific stimulus sequence in any block would be generated by one of four different undisclosed algorithms ("sources"). Participants were asked to rate, after every block, their inclination to avoid future blocks from the same source. We assumed that there would be endogenous variability both in brain activity and in reported avoidance tendencies, even though stimuli were in fact generated using a uniform procedure. We further assumed ratings would reflect the same internal factors that drove avoidance in our behavioral experiment. Whole-brain analyses evaluated within-subject correlations between block-related BOLD amplitudes and the subsequently assigned avoidance ratings. We expected to observe a positive correlation in control-related cortical regions.

Our analyses partialled out the influence of reaction time (RT) and error because these variables could plausibly influence both brain activity and avoidance ratings. Indeed, individual subjects showed positive correlations between avoidance ratings and the number of errors per block (mean $r = 0.50$, $t[9] = 10.25$, $P < 0.01$; mean error rate = 3.2%), but ratings spanned the full range of the scale even when only blocks free of errors were

Fig. 1. The demand selection task. In a behavioral test of the DST (*A*), participants repeatedly chose between two stimulus locations. Choices tended to shift toward the low-demand location over the course of an experimental run (*B*); *n* = 12. Total low-demand selection rates varied (49–96% across subjects), and the DST showed internal consistency (α = 0.79) across its eight runs. The same pattern occurred in the DST administered following fMRI Experiment 2 (*C*); *n* = 22. Here again, individuals differed (*D*); single-subject bias rates exceeded chance for 10 participants (red data series), but not for the remaining 12 (black data series). Error bars show SEM.

considered (76% of blocks on average) (Fig. 2). Ratings were also correlated with block mean RT (mean *r* = 0.29, *t*[9] = 5.93, *P* < 0.01) (Fig. S1). After separately modeling RT and error (Fig. 3 *A* and *B*), we observed significant correlations between block-related BOLD response and avoidance ratings in two anatomical clusters: one in left LPFC (90 voxels; peak *x* = −51, *y* = 12, *z* = 27), and a smaller region in right LPFC (34 voxels; peak *x* = 48, *y* = 9, *z* = 24; Fig. 3*C*).

All blocks demanded frequent task switching, with the specific number of switches (versus repetitions) per block ranging from 5 to 8. Within this range, the number of switches predicted RT (*F*[1,9] = 30.8, *P* < 0.01) but not avoidance ratings independently of RT (*F*[1,9] = 0.42). After RT and error were removed, the number of switches did not significantly correlate with BOLD response in any brain region. Thus our statistical control of RT succeeded in capturing variance associated with external task difficulty.

Fig. 2. Rating data from fMRI Experiment 1. Light bars show the mean number of blocks (out of 96, with SE) assigned each level of the avoidance rating scale (*n* = 10). Dark bars show the same for error-free blocks only. The top two categories were combined to create rating level 3.

Fig. 3. Group analysis results of fMRI Experiment 1 (*n* = 10). (*A*) Regions responsive to error commission included dorsomedial prefrontal cortex (PFC) and bilateral anterior insula. (*B*) Regions modulated by reaction time (RT) included dorsomedial and dorsolateral PFC, insula, precentral gyrus, thalamus, and posterior parietal cortex. Only positive effects are depicted in *A* and *B*. (*C*) In left and right lateral prefrontal cortex clusters, avoidance ratings were correlated with single-block BOLD amplitude estimates. Correlations in *C* were estimated after factoring out the effects of RT and error shown in *A* and *B*. (*D*) Avoidance rating-correlated regions found in a follow-up analysis that did not exclude the influence of error and RT.

In contrast to LPFC, DMFC activity showed no relationship to avoidance ratings in the whole-brain analysis. This was unexpected, given past findings linking DMFC to the monitoring of demand for cognitive control (22, 23). We took three steps to probe this null result more closely.

First, we examined a 33-voxel region of interest (ROI) centered on peak dorsal anterior cingulate coordinates reported in a previous study of performance monitoring (29). Signal in this ROI was positively related to RT and error in every subject (signed-rank *P* < 0.01) but was not additionally correlated with decision costs (*P* = 0.77).

Second, we used the RT parameter to identify task-activated clusters in both left LPFC and DMFC, taking the top 200 RT-related voxels in each region. We then directly tested each cluster's relationship to decision costs (Fig. 4). The left LPFC cluster was positively related to avoidance ratings (signed-rank *P* = 0.02), whereas the relationship in DMFC was nonsignificant with a negative trend (signed-rank *P* = 0.08).* LPFC showed a significantly greater relationship to decision costs than DMFC (signed-rank *P* = 0.01).

Third, we repeated the primary analysis, this time without removing the influence of error or RT. Clusters correlating positively with ratings were found in DMFC, as well as bilateral regions of LPFC, insula, and precuneus (Fig. 3*D*). Together, these results confirm that DMFC is related to overt performance, which in turn predicts reported costs. Indeed, DMFC could well code costs relating to moment-to-moment changes in behavior, as has been suggested previously (22, 29). However, DMFC—unlike LPFC—showed no relationship to the subjective evaluation of decision costs independent of overt performance.

Experiment 2

Our second experiment sought to confirm the relevance of LPFC to the evaluation of decision costs, with costs now measured directly in terms of observed avoidance behavior. Here we assumed that decision costs would vary not just over time but also across individuals. We leveraged individual differences in

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*The negative direction of this trend, although interesting, is difficult to interpret given that the common influence of RT has been regressed out (30). We focus our interpretation on the clear presence of performance-independent effects in LPFC and on the difference between the effects seen in LPFC and DMFC.

Fig. 4. Interregion comparison in Experiment 1. Task-activated clusters were identified in left lateral prefrontal cortex (LPFC) (*A*) and dorsomedial frontal cortex (DMFC) (*B*). Correlations between avoidance ratings and single-block BOLD amplitudes (i.e., the data shown in Fig. 3*C*) were spatially averaged in each cluster for every subject (*C*). The spatially averaged coefficients were greater in LPFC than DMFC, and differed from zero in LPFC only.

subjects' tendency to avoid the more demanding alternative in the DST (Fig. 1) and tested whether these differences were related to task-evoked brain activity.

Participants first performed both high- and low-demand versions of the decision-making task in the MRI scanner, with the element of free choice removed. Then, outside the scanner, participants completed the DST. In contrast to the first experiment, instructions to the participant in both phases of this study made no reference to the themes of cognitive demand or mental effort.

Consistent with previous work (22), the median rate of low-demand selections in the DST (61%) exceeded the chance rate of 50% (signed-rank $P < 0.01$; Fig. 1*C*). Importantly, and again consistent with precedent, individuals varied in the strength of this bias (range: 41–95%), and the DST was internally consistent in measuring this interindividual variability ($\alpha = 0.87$). For further analyses we divided participants into a high-avoidance group (individuals showing a significant bias in a signed-rank test across the eight DST runs; $n = 10$, $z \geq 2.15$), and a residual group with choice data falling closer to the indifference line ($n = 12$, $z \leq 1.30$; see Fig. 1*D*). We assume that our manipulation led to greater differential decision costs in individuals who showed the stronger bias. Accordingly, we predicted that the previously identified LPFC region would show greater differential task-related activity in these individuals.

To analyze the fMRI data we first contrasted brain activity in the high- vs. low-demand decision condition, while simultaneously modeling the effect of response errors (Fig. 5*A*). We then tested whether the high-avoidance group would show greater contrast values in left LPFC, the location of the largest

effect in the previous experiment. Small volume-corrected analysis, focusing on the region activated in Experiment 1, detected the expected group difference in a significant 45-voxel cluster (peak $x=-51$, $y = 12$, $z = 21$). Thus, differential engagement in left LPFC was indeed greater for individuals who went on to show a consistent behavioral bias, implying that they experienced greater differential decision costs. The same pattern was found if parameter values were spatially averaged across the left LPFC cluster identified in Experiment 1 (Fig. 5*B*); responses to the high- vs. low-demand task differed by a greater amount for high-avoidance participants.

As in Experiment 1, the relationship between LPFC activity and decision costs did not depend on RT. RT was greater in the high-demand condition for every subject (985 ms vs. 744 ms; signed-rank $P < 0.01$), and this difference was marginally greater in the high-avoidance group (268 ms vs. 218 ms; rank sum $P = 0.07$). However, even after contrast coefficients were regressed on differential RTs across subjects, the residuals remained greater for high-avoidance subjects in a significant 25-voxel LPFC cluster. (Figs. S2 and S3 for error-related brain activity, whole-brain exploratory analysis of group differences, and group differences in pupil diameter.)

As in Experiment 1, we tested the DMFC ROI drawn from ref. 29. This region showed no difference between groups (rank sum $P = 0.92$).

Discussion

We have examined the idea that decision-makers experience a motive to minimize internal decision costs. Although the impact of internal costs on choice behavior (2, 3) and cognition in general (4, 21, 31) has been widely considered, little is known about how such costs are registered or evaluated at the neural level. Our results identify a relationship between decision costs and activity in left LPFC. We found that activity in this region correlated with participants' self-reported avoidance tendency across epochs of a decision-making task (Experiment 1), and with directly observed rates of avoidance across individuals (Experiment 2).

Importantly, whereas cognitively demanding decisions may sometimes be accompanied by errors and slow RTs, performance differences per se do not account for the present findings. Given that RT itself has sometimes served to operationalize decision costs (10, 32), it is notable that the relationship between LPFC and cost still holds independent of RT.

Our finding counters the intuitive possibility that decision costs reflect overall mental workload or metabolic consumption throughout the brain (33–37). Our task engaged a constellation of brain regions consistent with past studies of task switching (25), and it would have been logically possible for internal costs to depend on activity fluctuations throughout this network. In fact, however, we observed the effect uniquely in LPFC, implying a specific role for this region and for the control processes it is believed to implement.

In particular, LPFC and another control-related region, DMFC, differed markedly in their relationship to decision costs after overt performance was accounted for. This occurred despite the fact that both regions were strongly activated by our experimental tasks, are consistently implicated with task-switching and with control demands in general, and moreover are functionally connected (18, 19, 25, 38, 39). Indeed, DMFC has been linked to the registration of effort-related costs by substantial indirect evidence (22).

Why might lateral and medial prefrontal regions have differed? Although our neuroscientific data do not uniquely specify the underlying cognitive variables, we can readily interpret our findings in light of established theories of PFC function. DMFC has been proposed to play a role in monitoring outcomes and information processing efficiency, whereas, in contrast, LPFC is thought to impose top-down control, ultimately serving to regulate perform-

Fig. 5. Group analysis results of fMRI Experiment 2 ($n = 22$). (*A*) Regions showing a greater BOLD response to high-demand than low-demand blocks. (*B*) Mean parameters (with standard error) spatially averaged over the left-hemisphere lateral prefrontal cortex cluster identified in Experiment 1 (shown in Fig. 3*C*). Task-related signal change in this region was greater for high-demand blocks (dark bars) than low-demand blocks (light bars), and this difference was greater in high-avoidance individuals (main effect of demand level: $F[1,20] = 34.52$, $P < 0.01$; interaction: $F[1,20] = 4.63$, $P = 0.04$).

ance (18). Although the monitoring role of DMFC may be closely tied to observable changes in error and RT, application of cognitive control may entail an additional internal cost.

This interpretation parallels conclusions from work on a seemingly very different topic: the perception of physical heaviness. In principle, the heaviness of an object held in the hand could be judged either on the basis of "bottom-up" sensory signals reflecting the object's downward force or "top-down" efferent signals engaged in supporting the object. Research has suggested that the latter play a predominant role (40). Analogously, decision costs might arise not only from bottom-up performance feedback, but also from top-down control engagement. Humans may experience a drive to be "frugal" in their exertion of cognitive control, alongside their motive to perform tasks quickly and successfully.

We have studied decision costs in simple, highly controlled laboratory tasks. An immediate question is thus whether the relevance of the present findings extends to more complex decisions, such as choices among multiattribute alternatives. In addition, we have focused on the tendency of decision makers to avoid high-cost decisions outright, but decision costs are also thought to drive strategy selection (41). For example, internal costs might motivate decision makers to choose less systematic strategies (2, 41) or to favor the strategies that best suit their personal abilities (11, 42). Internal costs might also supply a motive to employ "reactive" as opposed to "proactive" cognitive control strategies (43, 44). The role of prefrontally mediated costs in driving strategy selection is an attractive target for future investigation.

We have said little about subjective phenomenology. Decision costs might conceivably involve sensations of effort, self-awareness, boredom, fatigue, frustration, or risk. Here we remain agnostic to which of these variables is most relevant; we assume only that costs are reflected in measures of avoidance, and we focus on the neuroscientific correlates of these avoidance measures.

Future work might focus on individual difference variables, such as working memory capacity, or on clinical disorders viewed as involving heightened sensitivity to effort-related costs. One such disorder, clinical depression, has indeed been associated with increased task-evoked LPFC activity (45, 46). Outside the context of psychopathology, however, the motive to minimize internal decision costs might serve a beneficial purpose, guiding behavior toward maximally efficient tasks and strategies.

Methods

Participants. Participants were members of the Princeton University community. In the preliminary behavioral experiment, n = 12 (age 18–22, 7 females). In fMRI Experiment 1, n = 10 (age 18–34, 4 females), with one additional participant excluded because of high error (19.5%). In fMRI Experiment 2, n = 22 (age 18–30, 14 females); one additional participant misunderstood instructions during scanning and was excluded.

Demand Selection Task. For the initial behavioral test, the DST was programmed using E-Prime (Psychology Software Tools, Inc.). Choice cues appeared as circular patterned patches. Participants mouse-clicked a patch to reveal a colored number. Depending on the number's color, participants judged either its magnitude or parity, responding via left-hand keypress. There was a 250-ms intertrial interval; otherwise the task was self-paced. One choice cue repeated the previously shown color on 90% of trials (low-demand), whereas the other switched colors on 90% of trials (high-demand). Each subject completed eight 75-trial runs. Choice cues in each run were unique in appearance and location.

Choice cues were always separated by an angular distance of 45° along the perimeter of an imaginary circle centered on the monitor. The mouse cursor was initially positioned midway between the two cues on each trial. The mapping of specific cues to demand levels was counterbalanced across participants. DST internal consistency was assessed using Cronbach's α, treating the eight runs as subtests.

Experiment 1 Procedure. Computerized tasks for both fMRI experiments were programmed using the Psychophysics Toolbox (PTB) extensions for Matlab

(47, 48). Participants performed magnitude/parity task switching as described above, initially completing approximately 140 practice trials outside the scanner.

During scanning, trials were shown at 2-s intervals, grouped into 96 10-trial blocks. The same digit never appeared twice consecutively. The first color was chosen randomly; thereafter, colors switched five, six, seven, or eight times per block.

Participants were told that they would probably find some blocks harder than others, that difficulty would depend partly on the specific sequence of stimuli shown, and that the computer used four algorithms to construct the sequences. Participants did not know the source of any given block but were instructed to provide a rating, directly afterward, of their desire to avoid blocks from the same source. In making ratings, participants were instructed to consider the amount of aversive mental effort they had experienced.

Instructions were designed to elicit an event-by-event measure of participants' inclination to avoid the cognitive task. For this reason, instructions intentionally refrained from describing block-to-block differences in any detail.

The first trial of each block was preceded by a 1-s fixation cross. After the last trial the fixation cross returned for 1 s, followed by the rating prompt, which consisted of four horizontally arranged boxes marked "none," "a little," "some," and "a lot." The rating scale disappeared when a response was made, and the next block began 7–13 s later. Participants responded to the prompt by pressing one of four keys. It was explained that participants' indicated preferences would not influence future trials and that they should use the full range of the scale, for instance, responding "a lot" for blocks they preferred to avoid relative to others in the experiment.

The 96 experimental blocks were divided into eight runs of functional scanning, which yielded 1,616 functional volumes per participant.

Experiment 2 Procedure. Participants performed magnitude/parity task switching as described above. Participants initially viewed two rectangles to the left and right of the screen, one colored green and the other orange, which were described as decks of cards containing imperative stimuli. Participants pressed a left or right key to select a deck, then responded to a sequence of eight trials (at 2-s intervals) on the deck they selected. Importantly, participants were asked to choose each deck an approximately equal number of times over the course of the experiment, without using simple patterns (e.g., alternating). The deck choice procedure was adopted to test hypotheses regarding task anticipation, which are not discussed further in the present report.

One deck alternated between tasks (high demand), whereas the other deck repeated the same task for an entire block (low demand). The mapping of deck color to demand level remained constant for each participant (but was counterbalanced across participants), whereas the left/right positions of the decks reversed in successive scanning runs. Digits were shown on a gray field in the center of the selected deck. Results showed that subjects were successful in choosing the two decks equally often (mean low-demand selection rate, 0.48; range, 0.40–0.60).

The two decks appeared anew at the beginning of each block, following a 2- to 8-s blank interval. After an 8- to 14-s delay, white borders appeared, signaling participants to indicate their choice. Task trials began 2- to 8-s later. There were 48 task blocks divided among six scanning runs, yielding 948 functional volumes per subject.

Subjects performed the DST in a behavioral testing room after scanning was complete. Participants were instructed that, unlike during the scanning phase, they were free to choose one alternative more often if they developed a preference. Each participant's low-demand selection rates in eight 60-trial runs were evaluated in a signed-rank test against 0.50 to provide the basis for between-subjects fMRI analyses.

fMRI Acquisition and Preprocessing. MRI data for both experiments were acquired using a 3T Siemens Allegra scanner at Princeton University, and were processed and analyzed using AFNI (49), SPM (www.fil.ion.ucl.ac.uk/spm/), and Matlab.

An echoplanar imaging sequence acquired 34 3-mm oblique axial slices (no gap) with repetition time = 2 s, echo time = 30 ms, flip angle = 90°, and field of view = 192 mm yielding 3-mm isotropic voxels. An MPRAGE anatomical scan was acquired at the end of the session, consisting of 160 1-mm sagittal slices (TR = 2.5 s, TE = 4.38 ms, flip angle = 8°, field of view = 256 mm).

We performed slice acquisition time correction using Fourier interpolation and motion correction using a six-parameter rigid body transformation to coregister functional scans. Timepoints adjacent to large changes in motion parameters or spikes in spatially averaged global signal were excluded from analyses. A despiking algorithm was used to attenuate outliers in each voxel's time course. Data were spatially blurred until total estimated spatial autocorrelation was approximated by a 3D 6-mm FWHM Gaussian kernel. Signal in each voxel was intensity-normalized to reflect percent change.

Both experiments were analyzed using a general linear model (GLM). Baseline regressors included zero- through third-order polynomial trends and each run's spatially averaged global signal timecourse.

fMRI Data Analysis: Experiment 1. BOLD response amplitudes for individual error-free blocks were estimated in a GLM. The model also contained regressors for error trials, blocks containing errors, rating-selection events, and linear effects of individual-trial RT.

The resulting error-free block amplitudes in each voxel were converted to ranks and tested for correlation with numerical avoidance ratings (coding "none" as 1, "a little" as 2, and both "some," and, "a lot" as 3). This resulted in a correlation map for every subject, which reflected monotonic relationships between ratings and response amplitudes. A secondary analysis used the same procedure to test correlations between block amplitudes and the number of task switches per block.

Correlation maps were spatially normalized and tested in a group-level *t* test. Spatial normalization was accomplished by warping each subject's anatomical image to match a template in Talairach space (50) using a 12-parameter affine and nonlinear cosine transformation. This transformation was then applied to statistical maps. Second-level analyses treated subject as a random variable and were spatially masked to include only voxels with acceptable signal intensity in all subjects. Monte Carlo simulation was used to find a combined intensity and cluster-size threshold that controlled whole-brain α to 0.05 (single voxel $P < 0.01$, cluster extent ≥ 31 voxels).

fMRI Data Analysis: Experiment 2. GLM regressors of interest included the mean response to high-demand and low-demand task blocks, error trials, deck selection responses, and the visual onset of the decks at the beginning of each block.

Each subject's data yielded a contrast map representing high-demand vs. low-demand task performance. This map was spatially normalized, and differences between the two groups were assessed in individual voxels using a nonparametric rank sum test.

To improve sensitivity, analyses were restricted to a left PFC region corresponding to the largest cost-related cluster observed in Experiment 1 (Fig. 3C). A small-volume-correction search region of 225 voxels was defined by masking the Experiment 1 results at a liberal threshold (single voxel $P = 0.05$). A Monte Carlo simulation identified a cluster-size threshold that controlled alpha inside this search region to 0.05 (single voxel $P < 0.05$, cluster extent ≥ 17 voxels).

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