The neural basis of cost-benefit trade-offs in effort investment: a quantitative activation likelihood estimation meta-analysis

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Abstract

Prominent theories of cognitive effort-based decision-making posit that shared brain regions process both potential reward and task demand, supporting the idea that effort allocation are informed by a cost-benefit trade-off, weighing the expected benefits of successful control against the inherent costs of effort exertion. While the dorsal anterior cingulate cortex (dACC) has been proposed as a candidate region supporting this decision, it remains unclear whether dACC activity tracks rewards and costs as independent quantities, or it reflects the effort intensity worth the integrated costs and benefits. While recent accounts of dACC function posit a crucial role the region in negotiating cost-benefit trade-offs, empirical evidence for this account remains scarce across single studies. To address this, we conducted a systematic meta-analysis review of neuroimaging studies, using activation-likelihood estimation method to quantify brain activity across 45 studies (N = 1273 participants) investigating reward-guided effort. We found reliable recruitment of the dACC, putamen, and anterior insula for processing both larger rewards and increasing task demands. However, the dACC clusters sensitive to task demands and rewards were anatomically distinct with no significant overlap: caudal dACC activity tracked increasing task demands, while rostral dACC activity tracked increasing rewards. Critically, we also observed that caudal dACC activity tracked the integration of costs and benefits, compatible with mental effort intensity account. These findings suggest there are distinct signals for demand and effort in the dACC which are also integrated to support the decision to invest effort, supporting recent computational accounts of cost-benefit value integration in effort-based choice.

Keywords: Cognitive control, Effort, Reward, anterior cingulate cortex, fMRI,

Introduction

How do we decide whether pursuing a reward is worth the mental effort required to obtain it? On the one hand, the experience of cognitive effort exertion is aversive (and often avoided), yet, on the other hand, individuals must often engage in effortful thinking to obtain rewards. Consequently, our decisions to engage in (versus avoid) cognitively costly processing often present a conflict between two opposing goals: maximizing rewards and minimizing the associated effort costs. To this point, prominent theories of motivated control posit that cognitive effort allocation decision-making requires the integration of the benefits (e.g., rewards) tied to effort exertion, the costs of effort, and the likelihood of successful performance (Frömer et al., 2021; Kurzban et al., 2013; Shenhav et al., 2017; Silvetti et al., 2018). Indeed, a large and growing body of empirical work suggests that our decisions to allocate (versus withhold) effort result from an integration of costs and benefits. For example, reward incentives motivate cognitive effort investment (Otto & Vassena, 2021; Westbrook & Braver, 2015), particularly for individuals with large effort costs (da Silva Castanheira et al., 2021; Sandra & Otto, 2018). Further, the subjective value of rewards—as evidenced by individuals' choices between options with varying effort and reward levels—appears to be discounted by the effort required to earn these rewards (Chong et al., 2017; Otto & Vassena, 2021), and people will even opt for a physically painful sensation over the prospect of exerting high levels of cognitive effort (Vogel et al., 2020).

Influential theories suggests that the dorsal anterior cingulate cortex (dACC) plays a role in resolving these effort-reward trade-off by integrating specific neural signals representing both effort costs and anticipated rewards (Shenhav et al., 2013; Silvetti et al., 2018), with some debate regarding the dACC's functional role (Shenhav et al., 2017; Vassena et al., 2017, 2020).

However, despite behavioral findings supporting the idea of an effort-reward trade off, the functional role of dACC in coding reward, effort cost, and/or the integration thereof, is less clear.

In line with the predictions of cost-benefit accounts of dACC function (Shenhav et al., 2013; Silvetti et al., 2018), some studies suggests that the dACC encodes both reward prospects and task demands. The anticipation of rewards has been consistently associated with greater activity in the dACC, anterior insula, thalamus, and ventral striatum (i.e., Nucleus Accumbens & Putamen; Bartra et al., 2013; Diekhof et al., 2012; Knutson & Greer, 2008). However, these observed patterns of neural activity were not specific to performance-contingent rewards, suggesting a general role for the dACC in encoding reward information. More recently, a meta-analysis by Parro and colleagues (2018) investigated activation patterns underlying performance-contingent reward incentives, finding reliable BOLD activity in the dACC, anterior insula, inferior frontal sulcus, and inferior parietal lobule in response to rewards. While both the dACC and anterior insula have been linked to subjective feelings of motivation on cognitive tasks, only the dACC has been found to encode integrated incentive values when performing effortful tasks (Yee et al., 2021). A parallel line of work has identified regions that encode costs associated with increasing task demands either during preparation for tasks or during task performance. When exerting control, increasing task demands engage the dACC, posterior parietal cortex, anterior insula, and prefrontal cortex (Laird et al., 2005; Niendam et al., 2012). When anticipating effortful tasks, activity in the dACC increased as a function of the subjective valuation of effort costs (Chong et al., 2017). Thus, activity in the dACC could either encode the effort level to be invested i.e., the integrated costs and benefits of effort exertion (Chong et al., 2017; Shenhav et al., 2016; Silvetti et al., 2018) or simply encode a representation of task demands (Lopez-Gamundi et al., 2021).

Beyond simply tracking rewards and demand, the dACC has also been found to play a role in learning and monitoring task progress. For example, the dACC activity has been found to track to negative consequences of errors like negative feedback (i.e., response errors; Carter et al., 1998; Cole et al., 2009; Ito et al., 2003; Ridderinkhof et al., 2004), and pain (Jahn et al., 2016; Shackman et al., 2011). At the same time, the dACC has been found to play a role in monitoring the need for cognitive control (Botvinick, 2007; Venkatraman & Huettel, 2012), tracking prediction errors (Alexander & Brown, 2015; Brown & Alexander, 2017; Silvetti et al., 2011), and even coordinating effortful control over extended action sequences (Botvinick et al., 2001; Holroyd & McClure, 2015). Together, these findings suggest a role for the dACC in learning of control signal specification to obtain rewards or avoid punishment (Shenhav et al., 2016). Converging neurocomputational work on adaptive decision-making proposes that the dACC integrates costs and benefits through a meta-learning mechanism via interactions with catecholaminergic input from subcortical systems (the Reinforcement Meta Learner model; Silvetti et al. 2018). In this computational account, the dACC also contributes to the learning of optimal effort allocation over time (Verguts et al., 2015) and to other adaptive learning dynamics (i.e., control of learning rate, higher-order reinforcement learning, Silvetti et al. 2018). Importantly, most of these perspectives rely on the assumption that, to some extent, the dACC receives input signals indexing reward and cost to compute an integrated quantity (net value) that would guide decisions. This reward signal is supplied via midbrain dopaminergic input, as extensive work in animals has shown (Haber et al., 2006; Haber & Knutson, 2010). On the contrary, the source and neural representation of the cost signal remain highly debated (Holroyd, 2015; Kurzban et al., 2013; Musslick & Cohen, 2021; Wiehler et al., 2022). Whether the cost of cognitive effort is encoded by dACC, and to what extent a reliable signal representing the control

signal intensity based on the integration of the costs and benefits is traceable in dACC activity, remains unclear.

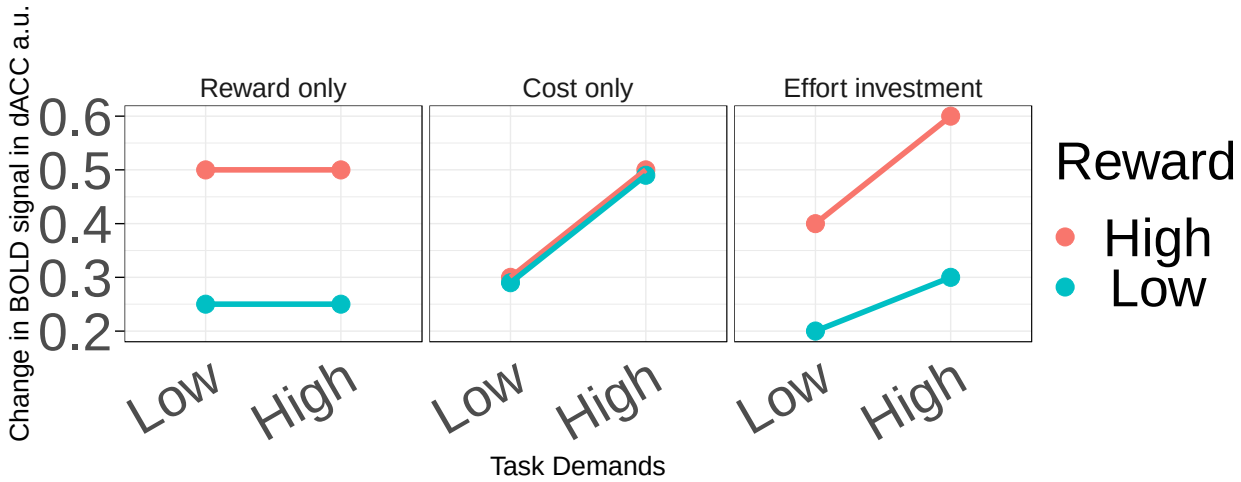

Figure 1 Hypothesized patterns of dACC BOLD signal based on what this signal is thought to reflect: costs only, benefits only, or the effort investment based on the expected value of control. For the reward model, where dACC activity is posited to only reflect reward prospects, BOLD signal is predicted to increase simply as a function of performance-contingent rewards. For the cost model, where dACC activity is posited to only reflect costs, BOLD signal is predicted to increase only as a function of task demands. And for the integration models, where dACC activity reflects the intensity of the control signal or effort to be invested, BOLD signal is predicted to increase in response to higher rewards and higher levels of task demands.

However, individual studies are limited in their ability to draw conclusions on the neural representation of rewards and effort, particularly due to heterogeneity in both the putative cognitive processes required by tasks, and the reward prospects used to study motivated behaviour. This variability across studies is especially relevant in the case of inconsistent findings, often leading to robust debates in the literature—for example, in the case of the dACC (Ebitz & Hayden, 2016; Vassena et al., 2017). Meta-analytic synthesis offers the opportunity to isolate reliable effects of interest, allowing for joint investigation of parametric manipulations of demand and reward levels across multiple studies (Yarkoni et al., 2010). Here, we used the activation-likelihood estimation meta-analytic technique (Eickhoff et al., 2012), synthesizing

brain activity across 45 studies, to examine whether the predictions of the cost-benefit account of dACC function are supported across diverse manipulations of cognitive effort and reward. By looking across studies that manipulated both demand level (i.e., effort cost) and performance-contingent rewards, the present meta-analysis allows us to examine whether aggregate dACC activity is associated with effort investment reflecting an integrated representation of costs and benefits, versus a representation of only costs (or only benefits).

Importantly, these different possibilities lead to contrasting hypotheses about the patterns of possible association between dACC activity, task demand and reward level (see Figure 1). If dACC activity only reflects performance-contingent rewards, BOLD responses should increase monotonically with larger rewards but not higher task demands (see Figure 1, left panel). And if dACC activity reflects only raw effort costs, BOLD responses should increase monotonically with higher task demands but not larger rewards (see Figure 1, middle panel). However, if dACC activity reflects the control signal intensity, i.e., effort to be invested, then BOLD responses should depend collectively on costs, and demands. For example, in the Expected Value of Control (EVC) model (Shenhav et al., 2013), dACC activity is posited to increase with larger rewards and higher task demands (i.e., scales positively with net value; see Figure 1, right panel; Silvestrini et al., 2022). Little work has jointly assessed the neural representations underlying processing both prospective rewards and cognitive demand overlap. Yet, studies who have jointly investigated rewards and task demands have only observed increases in dACC BOLD activity for both larger rewards and task demands (Vassena et al. 2014). However, this study may be limited in its ability to capture the net-value discounting computation, as they contrasted 2 demand levels with high overall accuracy (>90%), in so far that exerting effort was mostly

rewarding (see Figure 1). In sum, whether dACC simply tracks effort costs, or integrates reward and demand information into a net value has yet to be corroborated.

While two previous meta-analyses have found inconsistent results in overlapping regions of the dACC—finding that BOLD signal in the dACC decreases with increasing net value (Lopez-Gamundi et al., 2021), and increases as a function of available rewards (Parro et al., 2018)—we sought jointly and systematically examine task demands and rewards. Motivated by the inconsistency in the posited functional role of the dACC, the current meta-analysis aims to disentangle the common and unique patterns of activation observed across several fMRI studies which independently manipulate reward prospects tied to effort exertion, and task demands across a variety of operationalizations of cognitive demand and reward. Using this approach, we can assess i) the regions uniquely involved in processing rewards, ii) the regions uniquely involved in processing task demands and iii) the regions involved in both processes. We further assess the regions which track the interaction between reward and demand signals, encoding the integrated value of effort investment. Based on cost-benefit models of effort decision-making (Shenhav et al., 2013; Silvetti et al., 2018), we predict the dACC will not only serve to independently track the costs and benefits of effort but also serve to integrate these signals reflecting the effort level deemed worthy of investing.

Materials and Methods

Literature Search

We conducted a systematic review of functional magnetic resonance imaging (fMRI) cognitive control studies which experimentally manipulated either available rewards, task demand, or both. Our literature search and exclusion process are depicted in the flow chart in Figure 1. We searched for articles published prior to August 11th, 2022, on the online databases

PubMed/MEDLINE, Web of Science, and PsychINFO, with abstracts, titles, and keywords matching the following search string: ("REWARD*" OR "MONETARY INCENTIVE*" OR "MOTIVAT*" OR "INCENTIV*") AND ("COGNITIVE EFFORT" OR "MENTAL EFFORT" OR "COGNITIVE CONTROL" OR "EXECUTIVE FUNCT*" OR "WORKING MEMORY" OR "INHIBIT*" OR "SET SHIFTING" OR "SET-SHIFTING" OR "TASK SWITCHING" OR "TASK-SWITCHING" OR "LOAD" OR ”COGNITIVE LOAD" OR "DIFFICULT*" OR "EFFORT* " OR " DEMAND* ") AND ("FMRI" OR "FUNCTIONAL MAGNETIC RESONANCE IMAGING" OR "BRAIN IMAGING" OR “MRI”) AND ("HUMAN*" OR "PARTICIPANT*" OR "ADULT*” OR “SUBJECT*”). This search yielded 3318 articles. We further included 82 articles which were obtained from manually searching the reference list of previous coordinate-based meta-analyses on either reward processing or effortful control (see Figure 1) (Diekhof et al., 2012; Laird et al., 2005; Lopez-Gamundi et al., 2021; Parro et al., 2018).

We screened the identified articles for the following inclusion criteria: the studies must be 1) empirical investigations (i.e., not review articles); 2) employ fMRI; 3) be performed in healthy young adult humans; 4) estimate effects using GLMs over the whole brain with reported Montreal Neurologic Institute (MNI) or Talairach coordinates; 5) and report main effects of reward or demand on BOLD activity. To be included in the analysis, studies had to elicit a trade-off between rewards and effort by independently manipulating both reward incentives and demand levels within subjects. For the reward manipulations, the reward had to be 1) instrumental (i.e., based on responses) 2) performance-contingent (i.e., not random) 3) mediated by the successful engagement of cognitive processes (e.g., attention, working memory, response inhibition, etc.) as opposed to physical exertion and 4) not serve as a distractor (e.g., Failing &

Theeuwes, 2017). For the demand manipulations, demand level had to be manipulated experimentally—note, here we assume increasing task demands require greater effort to resolve (Shenhav et al., 2013). Finally, we excluded any studies which did not provide coordinates estimated in a healthy young adult population (i.e., clinical, or older adults) or used ROI analyses.

Using these criteria, a total of 45 articles were accepted, with 46 independent samples as one paper reported 2 experiments (Ursu et al., 2008). It should be noted that we obtained two independent sets of contrasts from one article (Kouneiher et al., 2009) as it reported the effects of both response preparation. Finally, one study collapsed analyses across young adults and adolescents which we chose to include (Magis-Weinberg et al., 2019).

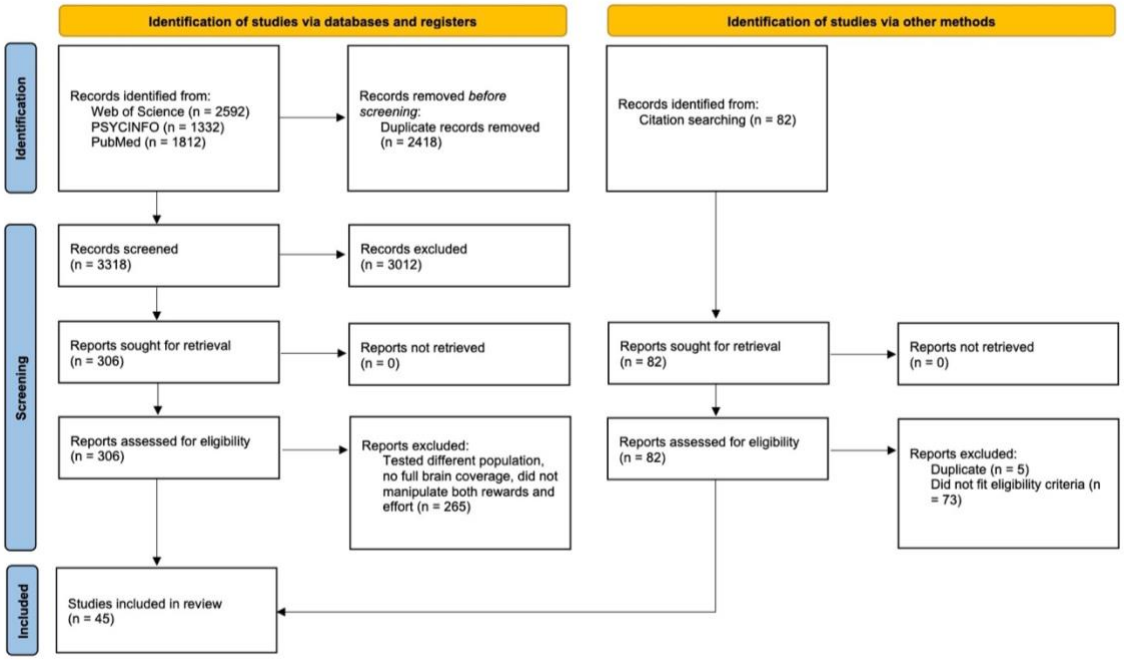

Figure 2 Flowchart of article screening and selection, following PRISMA guidelines. Adapted from (Page et al., 2021) Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 2021;372:n71. doi: 10.1136/bmj.n71

Coordinate based meta-analysis

We ran a coordinate-based meta-analysis using the foci (i.e., coordinates in significant clusters) reported in the identified studies. To ensure all coordinates were in the same stereotaxic space, we transformed the coordinates reported in Talairach space to MNI space using the FSL transformation applied in GingerALE (Eickhoff et al., 2012). The *x* (left vs right) and *y* (anterior vs posterior) coordinates of one paper was identified as inverted based on the anatomical labels reported (Chikara et al., 2018), and accordingly, we multiplied these coordinates by -1 to convert them back into standard space. We excluded any coordinates identified to be outside the brain, this resulted in the removal of 3 foci (2 from Reward contrasts and 1 from Control contrasts), and a final sample of 429 foci for rewards and 460 foci for task demands (see Table 1). In addition, our literature search revealed 32 foci associated with deactivations for increasing reward prospects, 16 each from 2 studies (Krebs et al., 2012; Pochon et al., 2002) and 8 foci increasing task demands (Krebs et al., 2012). We opted to exclude these coordinates from the analysis given our specific interest in identifying regions encoding raw effort costs and reward value.

We preformed meta-analyses using GingerALE (3.0.2; Eickhoff et al., 2009, 2012; availalble at www.brainmap.org/ale). The Activation Likelihood Estimation (ALE) algorithm computes convergence of activation across coordinates reported from whole-brain analysis. To do so, ALE models the spatial uncertainty of coordinates using 3-dimensional full width at half maximum (FWHM) gaussian kernels centered at the foci, with a width inversely proportional to the sample size. Thus, coordinates from studies with larger sample sizes are modeled with smaller Gaussian kernels, reflecting a more reliable approximation of the true spatial location of BOLD activity. Conversely, coordinates from studies with smaller sample sizes are modeled with larger Gaussian kernels, reflecting the uncertainty in the precise spatial location of activity.

Using these activation likelihood estimates, GingerALE computes the overlap of activation probabilities and determines voxels where there is a convergence significantly higher than expected if results were independently distributed. The resulting images can then be corrected for multiple comparisons, using cluster correction. For the purposes of our analysis, we chose a relatively conservative threshold ($p < 0.05$ FWE; 5000 permutations, $p < 0.001$ cluster forming threshold).

To test whether both rewards and effort reliably engage the dACC, we estimated three separate meta-analyses on studies manipulating 1) rewards (36 studies, 920 participants); 2) task demands (38 studies, 1095 participants) and 3) reported interactions between rewards and task demands (15 studies, 418 participants). Additionally, we ran a conjunction/contrast analyses comparing reward to effort. Conjunction between two sets of coordinates can be assessed using the voxel-wise minimum value of the activation likelihood estimates (Eickhoff et al., 2012). Contrasting the two sets of coordinates is done by subtracting the activation likelihood estimates between images and calculating voxel-wise Z-scores of the differences against a permuted distribution (Eickhoff et al., 2012). These resulting Z-scored differences are then subject to cluster analysis. For our contrast analysis, we conducted 100,000 permutations, and set a threshold $p < 0.01$ FWE and minimum cluster size of $300mm^3$.

Given the diversity of the studies included, both in terms of cognitive task and reward manipulation, it is critical that statistical power be considered. Currently, the inclusion of a minimum of 17-20 studies in a meta-analysis is recommended to ensure sufficient power to detect valid results, and prevent results from being driven by a single experiment (Eickhoff et al., 2016; Müller et al., 2018). Our literature search revealed 45 studies (46 experiments), reporting a total of 36 reward contrasts and 38 demand contrasts of interest, resulting in 457 reward-related

foci and 491 demand-related foci (see Table 1). Of the 46 experiments included, 34 reported both reward and effort contrasts. A total of three reward contrasts, and one demand contrasts found no significant foci for their contrast of interest. In terms of reward contrasts, most reward contrasts (21 studies) compared reward to no reward, while fewer reported a contrast between high and low reward (14 studies) only three studies reported a parametric effect of reward, and one used a repetition suppression paradigm (see Table 2). Regarding effort contrasts, the most common method for manipulating task demands involved response inhibition (20 studies), followed by working-memory (12 studies), attention (7 studies) and task switching (6 studies; see Table 2). Two additional papers used arithmetic of different difficulty levels to manipulate task demands (Hernandez Lallement et al., 2014; Vassena et al., 2014). Critically, of the experiments which tested for reward effects on response times or accuracy (45 experiments), 9 tested accuracy difference, 16 tested response-time differences, 15 tested both, and 3 used effort discounting choice paradigms; most experiments reported significant improvements in task performance with increasing rewards (36 of 45 studies).

Results

BOLD response to rewards

First, we sought to test which brain regions reliably encoded information about performance-contingent rewards. To this end, we assessed the converging patterns of brain activity in response reward contrasts and observed six clusters sensitive to performance-contingent reward incentives whereby activity was found to increase in response to larger reward prospects. Our analysis revealed six clusters of activity across regions typically associated with reward-related processing (Bartra et al., 2013; Diekhof et al., 2012; Knutson & Greer, 2008)—including the ventral striatum, the medial prefrontal, and Insular cortex. Bilaterally, we observed

two clusters encompassing the putamen and caudate, as well as a second cluster in the rostral portion of the dACC. We also found reliable patterns of activation in the right anterior insula and left inferior occipital cortex.

BOLD response to task demand

Next, we sought to test which brain areas encode raw effort costs by identifying regions where the activity shares a positive, monotonic relationship with increasing task demands. Our analysis revealed a reliable pattern of brain activity for increasing task demands which consisted of nine clusters across regions typically associated with cognitive control (Laird et al., 2005; Niendam et al., 2012)—the prefrontal, dorsal anterior cingulate, and parietal cortices. On the lateral aspect, we found two clusters in the left lateral PFC, one extending from the left middle frontal gyrus to the left precentral gyrus, and another located more dorsally in the left middle frontal gyrus, and one cluster in the right inferior frontal gyrus extending posteriorly to the precentral gyrus. Bilaterally, we observed robust activation of both the superior parietal lobule extending into the precuneus and the anterior insula. On the medial aspect of the brain, we observed reliable activation of the medial frontal gyrus, extending from the dACC into the Supplementary Motor Area. In the right hemisphere, our analysis revealed a reliable cluster in the thalamus.

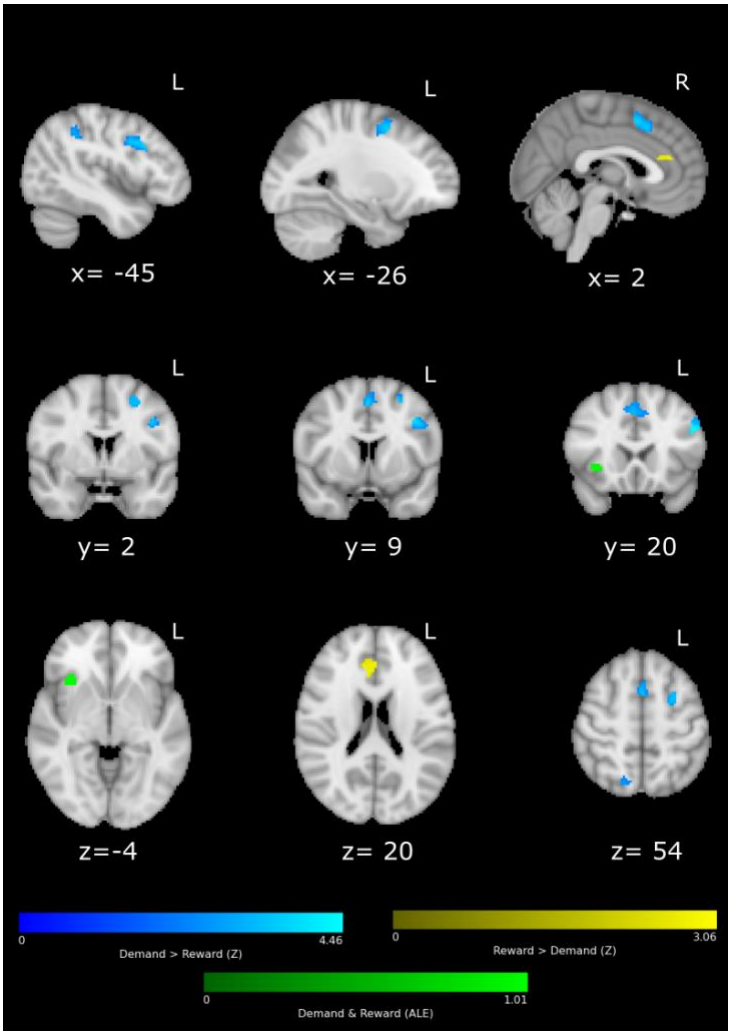

Figure 3 Results of reward and effort ALE meta-analysis. Brain areas showing converging activation for both increasing reward prospects and task demands, plotted in the volume (MNI152) with shades of green. Brain areas more activated by increasing task demands than reward prospects plotted in the volume (MNI152) with shades of blue . Brain areas more activated by increasing reward prospects than task demands plotted in the volume (MNI152) with shades of yellow.

Differences in BOLD response between reward versus demand

Next, we evaluated the strength of evidence for the effort cost (Lopez-Gamundi et al., 2021) and integrated cost-benefit (Chong et al., 2017; Shenhav et al., 2013; Silvetti et al., 2018) accounts of dACC activity by assessing whether the patterns of unique and overlapping activity between reward- and demand-elicited activity. To assess the unique patterns of activity, we

contrasted BOLD responses which were more responsive to increasing reward prospects than increasing task demand. Our analysis revealed a cluster of 728mm^3 in the rostral aspect of the dACC which was reliably engaged by increasing reward prospects more than increasing task demands (see Table 3, and yellow cluster depicted in Figure 3). Contrasting demands level with reward level, our analysis revealed a total of six clusters in which activity was more reliably engaged in processing increasing task demands than increasing rewards (see Table 3; and blue clusters depicted in Figure 3), including a cluster of 2056mm^3 in the caudal portion of the dACC extending into the Supplementary Motor Area (see Table 3, and blue clusters depicted in Figure 3). On the lateral aspect of the frontal lobe, our analysis revealed two clusters in the left middle frontal gyrus which extended anteriorly from the precentral gyrus, a second cluster on the more superior portion of the middle frontal gyrus and left inferior parietal lobule. Caudally, we observed three clusters more active in response to task demands than rewards in the left Precuneus, and bilaterally in the Inferior Parietal Lobule. In terms of overlapping patterns of BOLD responses, our conjunction analysis revealed one clusters where foci associated with both reward and task demand manipulations were found to converge (see Table 3, and green clusters depicted in Figure 4). We observed reliable overlap between reward- and demand-elicited BOLD activity in the right anterior insular cortex. Together, our analyses suggest a distinction between the dACC responses to rewards and task demands: across the task demand contrasts, foci converged in the caudal portion of the dACC, extending into the SMA, whereas reward foci converged in the rostral portion of the dACC. This distinction between reward and demand in the dACC provides preliminary evidence in favor of an effort cost representation as it is consistent with a positive relationship with task demands and no relationship with reward. Yet, these results

alone cannot differentiate between the posited functional roles of activity in the dACC without considering integrated value of rewards and task demands.

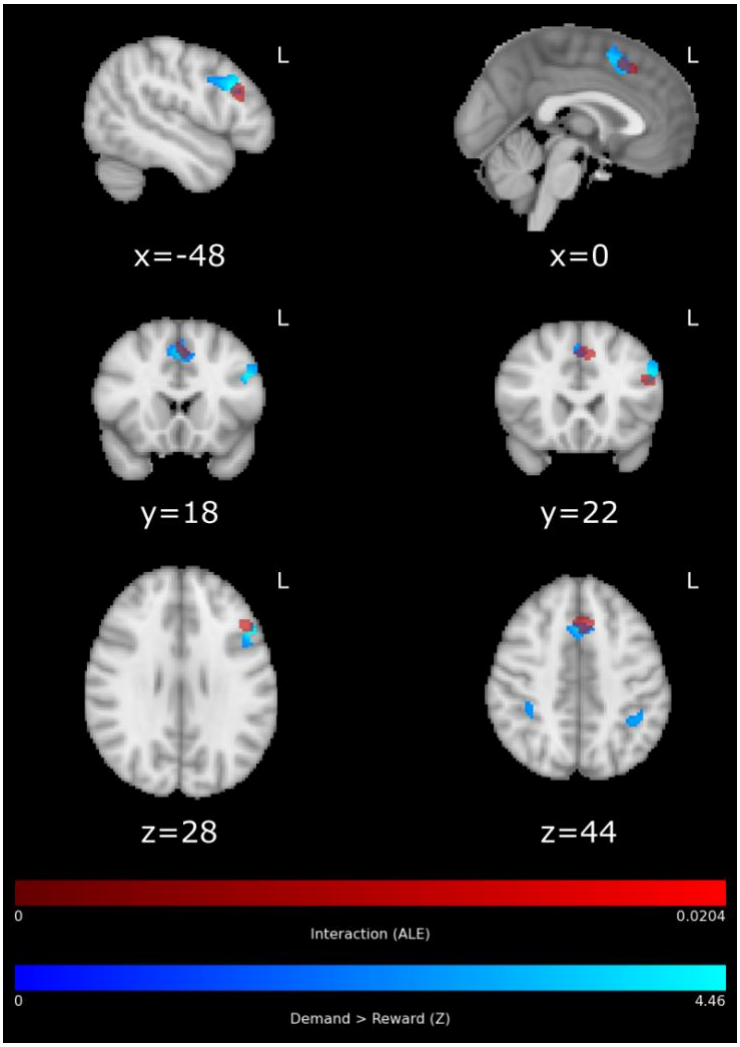

Figure 4 Results of interaction (reward X effort) ALE meta-analysis. Brain areas showing converging activation for the interaction between rewards and effort plotted in the volume (MNI152) with shades of red. Brain areas activated by task demands plotted in the volume (MNI152) with shades of blue. Blue clusters were rendered transparent to depict the overlap between clusters.

BOLD response to integrated cost-benefits

Next, we explored whether there were any reliable patterns of activation associated with the integrated cost-benefits of effort across 15 experiments (152 foci from 418 participants)—as

indexed by BOLD response correlated with either computed subjective value in effort discounting tasks (Chong et al., 2017; Massar et al., 2015; Westbrook et al., 2019) or by interactions between reward and task demands in reward-motivated control studies. Of interest, we sought to assess the strength of evidence that the dACC, beyond encoding the costs associated with increased cognitive effort, also encodes the effort level to be invested based on the integrated costs-benefits of exertion. Our analysis revealed two clusters in the frontal lobe, one on the lateral aspect encompassing the middle frontal gyrus, and one on the medial aspect extending form the SMA to the dACC (see Table 4, see the clusters depicted in warm colours in Figure 4). These two clusters representing the interaction between reward and demand were also found to partially overlap (568 mm^3 for the medial cluster and 152mm^3 for the lateral cluster) with the clusters previously identified as responsive increasing demands (Demand > Reward; see Figure 4). The first cluster, located in the medial frontal lobe, contained coordinates from four studies (Bahlmann et al., 2015; Padmala & Pessoa, 2011; Westbrook et al., 2019), three of which reported BOLD responses consistent with cost-benefit integration (see Figure 1 right panel). The second cluster, located in the lateral frontal lobe, contained coordinates from four studies (Chong et al., 2017; Leong et al., 2018; Padmala & Pessoa, 2010, 2011), two of which reported BOLD responses consistent with cost-benefit integration (see Figure 1 right panel). Thus, our analyses suggest that there is moderate evidence in support of dACC activity reflecting the integration of costs and benefits.

Discussion

A key tenet of recent neurocomputational accounts of effort-based decision-making proposing that activity in brain regions like the dACC reflect a trade-off between the costs and benefits of effortful cognitive processing (Silvetti et al., 2018; Verguts et al., 2015). Yet, the

precise functional role of the dACC in effortful behaviour remains unresolved as activity could simply reflect effort costs which covary with effort outlay (Vassena et al., 2017). Here, we carried out a meta-analysis of neuroimaging studies jointly manipulating cognitive demand and reward incentives, and assessed whether dACC activity reflects rewards, effort costs, or an integration of the two decision variables. Our analyses revealed that increasing task demands were associated with increasing activity the dACC, as well as both the lateral and parietal cortices—replicating extant work (Laird et al., 2005; Niendam et al., 2012). The prospect of larger reward was also observed to engage the dACC. Yet, we did not observe reliable overlap between the subregions of the dACC which coded for reward and effort. Instead, our analyses revealed two dissociable regions within dACC — the caudal portion tracking demand, and the rostral portion tracking reward, supporting the view that effort costs and rewards are represented separately in the brain. In support of an integrative cost-benefit signal, we found evidence for reliable engagement of the caudal dACC (Chong et al., 2017; Shenhav et al., 2013; Silvetti et al., 2018; Soutschek & Tobler, 2020). Together, these results suggest anatomical specificity for the activity of the dACC: activity in the rostral region reflects increasing reward prospects, whereas activity in the caudal region reflects increases in task demand and an integrated signal reflecting both task demands and reward prospects, but rewards alone are not sufficient to elicit increased caudal dACC activity.

Broadly, our results provide a clearer understanding of the dACC's role in motivating effortful action. Prominent theories of cognitive effort support cost-benefit models where the control signal intensity is determined by the dACC which integrates both information about available rewards and the cost associated to exerting control (Shenhav et al., 2013, 2016). aligned with extant work, we provide indication for a role of the dACC in tracking both effort

costs (Lopez-Gamundi et al., 2021) and the control signal intensity afforded by the integrated value of effort and reward (Chong et al., 2017; Shenhav et al., 2013, 2016; Silvetti et al., 2018). Despite the observed integration in the dACC, we did not find a reliable overlap between for large reward and high demand in the dACC, unlike Vassena et al. (2014). Perhaps this previous overlap was observed due to the overall high accuracy of the two contrasted demand levels, thereby making effort exertion mostly rewarding. This raises the possibility that the probability of reward given effort exertion may also modulate dACC activity (Frömer et al., 2021; Grahek et al., 2022; Otto et al., 2022). At the same time, previous work which characterizes the dACC as playing a critical role in monitoring the need for cognitive control (Botvinick, 2007; Venkatraman & Huettel, 2012), but also linked to individuals' avoidance of effort (McGuire & Botvinick, 2010), and effort-discounted rewards (Chong et al., 2017). Indeed, the results of our meta-analysis suggest that region of the dACC tracking the integrated cost-benefit signal also overlapped with the region tracking increasing task demands. Perhaps this overlap reflects the monotonic relationship between task demands and effort investment we assumed—that is, to achieve equivalent performance on tasks of differing demands, greater effort should be expended on the more demanding task. Given that the region tracking integrated cost-benefits and task demands overlapped, this suggests that a great deal of the high demand tasks used in this meta-analysis were difficult but achievable i.e., high effort was invested for harder tasks. However, this operationalization, which underlies a deal of research on cognitive effort, may not always be satisfied when greater effort does not yield better performance or when participants are given impossible tasks (Otto et al., 2021; Silvestrini et al., 2022).

At the same time, converging neurocomputational work suggests that the dACC contributes to learning the optimal control signal specification (Silvetti et al., 2018; Verguts et

al., 2015) by also tracking negative feedback (i.e., response errors) (Carter et al., 1998; Cole et al., 2009; Ito et al., 2003; Ridderinkhof et al., 2004). Recent work has outlined the importance of response efficacy—the relationship between effort and performance—in the decision to expend effort (Frömer et al., 2021). Under certain conditions, increasing effort allocation need not yield improved task performance implying a non-monotonic relationship between effort and performance. For example, for an impossible task where greater exertion would not improve performance, participants may choose to withhold effort. Indeed, some previous work has implicitly taken advantage of the marginal value of effort by contrasting performance-contingent to random rewards (Frömer et al., 2021; Shenhav et al., 2013; Späti et al., 2014). On this view, effort should only be invested when increasing effort investment confers larger performance benefits—i.e., the marginal value of effort (Otto et al., 2021). This distinction between effort and demand is reified in established accounts of motivated behavior such as Motivation intensity theory (Brehm & Self, 1989) which posit that the prospect of larger rewards does not unwaveringly improve performance but may depend on the efficacy of effort exertion in improving task performance. As such, previous work has noted performance decrements in response to larger reward prospects (Lee & Grafton, 2015). Cost-benefit models, which suggest increasing dACC reflects a license for effort, predict that activity in the dACC should vary depending on the response efficacy (Frömer et al., 2021; Shenhav et al., 2013). When the task is feasible at high demand levels, dACC activity should grow monotonically with task demands. When the task is impossible (i.e., high demand), dACC activity should elicit an inverted-U pattern, with a drop in engagement when demand is too high. Together, these predictions could explain how increases in task demand—which purportedly decrease the net value of effort—were associated with both increases and decreases in dACC activity in the literature. Beyond

dACC activity, other physiological measures like cardiovascular reactivity (see Wright, 2008 for discussion), pupil dilation (da Silva Castanheira et al., 2021), and facial muscle activity (Cacioppo et al., 1985; de Morree & Marcora, 2010; Van Boxtel & Jessurun, 1993) have been proposed as a method for indirectly measuring effort exertion. To reconcile these conflicting findings regarding the functional role of the dACC in effortful behaviour, future work should approach triangulation by jointly considering rewards, task demands and efficacy alongside neural activity, and psychophysiological measures of effort exertion.

It is also worth noting that the studies examined in this meta-analysis were constrained to those which used monetary incentives to motivate cognitive effort. Beyond cognitive control, previous work has found evidence for the dACC's involvement in processing and integrating both primary and secondary rewards (Yee et al., 2021). Similarly, the dACC has been found to integrate information about physical effort (Chong et al., 2017), pain and negative affect (Shackman et al., 2011). While cost-benefit models posits that the dACC integrates signals reflecting general costs and benefits, more work is needed to understand whether this pattern generalizes to other stimuli—particularly as there is some evidence for an anterior-posterior gradient of functional specialization from strategic to response-related conflict (Alexander & Brown, 2015; Venkatraman et al., 2009). The results of our reward-demand contrast analysis—in which the rostral portion of the dACC was found to respond more reliably to rewards while the caudal portion responds to demand—coincides with previous work which has also functional specialization of the dACC: a cognitive-affective gradient moving from caudal to rostral dACC (Bush et al., 2000). However, these distinctions have been inconsistent as others have found cognitive demand, affect and pain to overlap in the same region (Shackman et al., 2011). Thus, more work is needed to better understand the functional organization of the dACC.

The decision to invest effort is thought to rely on the coordinated activity between several brain regions (Ullsperger et al., 2014). While the literature as well as theoretical developments have strongly focused on ACC, empirical evidence indicates that other region may be sensitive to both manipulations of reward and effort and can play a role in resolving cost-benefit trade-offs. For example, the LPFC is thought to be involved in maintaining task relevant information in working-memory (Braver, 2012; Burgess & Braver, 2010) and executing cognitive control more generally (Miller & Cohen, 2001). While we found the LPFC was reliably engaged by increasing task demands suggesting a role in cognitive control implementation, we also found that the LPFC was sensitive to integrated effort-reward signals. Aligned with these results, recent work suggests the lateral prefrontal cortex (LPFC) may encode the capacity to successfully meet task demands, thereby representing the probability of successfully receiving rewards (Soutschek & Tobler, 2020). The anterior insula, often coactive with the dACC (Bartra et al., 2013; Diekhof et al., 2012; Parro et al., 2018), is also thought to be engaged in monitoring the need for control (Shenhav et al., 2016). Supporting this view, we found anterior insula was reliably engaged by both increasing task demands and reward prospects—suggesting a broader role of the region in processing salient events (i.e., arousal; Uddin, 2015) and subjective awareness (Craig, 2002), both of which are foundational to effort allocation. Together, these results suggest a role for the anterior insula in monitoring one's current state and detecting changes in the need for control (Nelson et al., 2010) and a role in cognitive processes more generally (Uddin et al., 2014). The ventral striatum, although typically thought of as a reward-processing region (Diekhof et al., 2012), has been shown to be sensitive to effort costs in the absence of rewards (Schouppe et al., 2014; Vassena et al., 2014). In terms of the Basal Ganglia, the Ventral Striatum was reliably engaged in processing rewards and effort whereas an overlap was not found in the dACC.

Previous work has shown a negative coupling between reward-related processing in the ventral striatum and dACC activation (Botvinick et al., 2009). Together with the literature, our results support the notion that the dACC along with a coordinated set of regions are involved in the integration of effort costs and the benefits conferred by rewards. Yet, given ALE-coordinate based analyses preclude network interpretations, our results are limited in their ability to draw conclusions on the coordination of regions. Thus, future work should aim to disentangle the underlying network dynamics contributing to the decision to expend effort.

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Table 1 List of reward and effort studies meeting criteria

First Author	Year	N	Study Type	Reward Contrast	Cognitive Task Domain	Reward Effect	N Foci Reward	N Foci Effort	N foci Interaction
Aarts	2010	20	Execution	High vs. Low	Task Switching	Y	11	14	
Alexander	2010	24	Execution	High vs Low	Response Inhibition	N	0	1	1
Asci	2019	22	Execution	Reward vs None	Response Inhibition	Y	0	6	3
Bahlmann	2015	20	Execution	High vs. Low	Task Switching	Y	9	13	2
Belayachi	2015	18	Execution	Reward vs None	Working-Memory	N	4	9	
Boehler	2014	16	Execution	Reward vs None	Response Inhibition	Y	12	29	
Brown	2007	21	Execution	High vs. Low	Response Inhibition	N	1	0	
Bruening	2018	22	Execution	Reward vs None	Working-Memory	Y	9	20	
Charron	2010	32	Execution	High vs. Low	Working-Memory	Y	7	2	
Chikara	2018	20	Execution		Response Inhibition	Y		12	16
Cho	2022	33	Execution	Reward vs. None	Working-Memory	Y	28	31	
Chong	2017	34	Decision-making		Attention	Y			7

First Author	Year	N	Study Type	Reward Contrast	Cognitive Task Domain	Reward Effect	N Foci Reward	N Foci Effort	N foci Interaction
Dixon	2012	15	Execution	Repetition Suppression Reward (novel > repeated)	Attention	Y	10	10	
Gaillard	2019	23	Execution	Reward vs None	Working-Memory	Y	16	1	12
Hernandez Lallement	2014	30	Execution		Arithmetic	N		14	
Ivanov	2012	16	Execution	High vs. Low	Response Inhibition	Y	7	9	6
Jimura	2010	31	Execution	Reward vs None	Working-Memory	Y	2		
Kostandyan	2020	25	Execution	High vs. Low	Response Inhibition	Y	10	6	
Kouneiher	2009	16	Execution		Task Switching			1	
Kouneiher	2009	16	Execution	High vs Low	Task Switching	Y	3	1	
Krebs	2012	14	Execution	Reward vs None	Attention	Y	23	21	7
Krebs	2011	18	Execution	Reward vs None	Response Inhibition	Y	23		
Lee	2017	18	Execution	Reward vs None	Response Inhibition	Y	14		
Leong	2018	40	Execution	Reward vs None	Response Inhibition	Y	14	37	12

First Author	Year	N	Study Type	Reward Contrast	Cognitive Task Domain	Reward Effect	N Foci Reward	N Foci Effort	N foci Interaction
Locke	2008	16	Execution	Reward vs None	Response Inhibition	Y	19		
Longe	2009	10	Execution	High vs. Low	Working-Memory	Y	6	4	
Luethi	2016	88	Execution	Reward vs None	Response Inhibition	Y	54	15	
MagisWeinberg	2019	50	Execution	Reward vs None	Working-Memory	Y	25	14	
Massar	2015	23	Decision-making		Response Inhibition	Y			33
Mizuno	2008	14	Execution		Working-Memory	N		31	
Nigam	2021	21	Execution	Reward vs None	Response Inhibition	Y	0	3	
Orr	2019	19	Execution	Reward vs None	Task Switching		26	10	
Padmala	2010	34	Execution		Response Inhibition	Y		12	7
Padmala	2017	57	Execution	Reward vs None	Attention	Y	6	21	12
Padmala	2011	50	Execution	Reward vs None	Response Inhibition	Y	29	11	19
Paschke	2015	115	Execution		Response Inhibition	Y		12	

First Author	Year	N	Study Type	Reward Contrast	Cognitive Task Domain	Reward Effect	N Foci Reward	N Foci Effort	N foci Interaction
Pochon	2002	6	Execution	Parametric effect of Reward	Working-Memory	N	11		
RosellNegre	2017	37	Execution	Parametic effect of reward	Response Inhibition	Y	1	11	
Soutschek	2015	20	Execution	High vs. Low	Response Inhibition	Y	3	4	5
Stoppel	2011	18	Execution	High vs. Low	Attention	Y	4	10	
Taylor	2004	12	Execution	High vs. Low	Working-Memory	N	6	16	
Ursu	2008 (Exp2)	17	Execution	Reward vs None	Attention	Y	19	5	
Ursu	2008 (Exp1)	19	Execution	Reward vs None	Attention	Y	16	4	
Vassena	2014	22	Execution	High vs. Low	Arithmetic	N	8	11	
Wang	2019	24	Execution	High vs. Low	Task Switching	Y	4		
Westbrooke	2019	21	Decision-making	Parametric effect of reward	Working-Memory	Y	9	15	10
Wilbertz	2014	49	Execution	Reward vs None	Response Inhibition	N	8	45	

Table 3 Conjunction and difference of the ALE meta-analysis for demands and effort. For each coordinate, region label, hemisphere (right, left or bilateral), Brodmann area, MNI coordinates, ALE maxima, *p* values, *Z* values, cluster size (mm^3), and number of studies are provided.

Brain Region	**Hemi**	**Cluster No.**	**x**	**y**	**z**	**N Studies (n Foci)**	**Volume (mm^3)**	**Studies in Cluster**
Reward & Control								
Insula	R	1	34	22	-4	6 (6)	416	Cho et al., 2022; Ivanov et al., 2012; Krebs et al., 2011; Boehler et al., 2014; Magis-Weinberg et al., 2019; Westbrook et al., 2019;
Reward > Control								
ACC	R/L	2	8	36	24	5 (5)	748	Boehler et al., 2014; Kostandyan et al., 2020; Bahlman et al., 2015; Luethi et al. 2016; Magis-Weinberg et al., 2019
Control > Reward								
Middle frontal gyurs	L	2	-48.4	19.8	28.2	9 (11)	2368	Bahlman et al., 2015; Mizuno et al., 2008; Vassena et al., 2014; Kostandyan et al. 2020; Kouneiher et al., 2009; Luethi et al., 2016; Leong et al., 2018; Paschke et al., 2015; Wilbertz et al., 2014
Supplementary Motor, dACC	L/R	4	2	12	50	7 (10)	2056	Westbrook et al., 2019; Krebs et al., 2012; Ursu et al., 2008;

								Lallement et al., 2014; Taylor et al., 2004; Wilbertz et al., 2014; Padmala et al., 2011
Middle frontal gyurs	L	5	-38	6	51	3 (3)	864	Belayachi, et al. 2015;Wilbertz et al., 2014; Padmala et al. 2010
Inferior Parietal Lobule	L	6	-38	-48	40	4 (4)	848	Cho et al., 2022; Luethi et al., 2016; Boehler et al. 2014; Lallement et al., 2014;
Inferior Parietal Lobule	R	7	38	-42	40	4 (4)	568	Cho et al., 2022; Orr et al., 2019; Ivanov et al., 2012; Padmala et al., 2010
Precuneus	R	8	14	-70	52	1 (1)	304	Aarts et al., 2010

Table 4 The ALE meta-analysis for coordinates representing the interaction between rewards and demands. For each coordinate, region label, hemisphere (right, left or bilateral), Brodmann area, MNI coordinates, ALE maxima, cluster size (mm^3), and number of studies are provided.

Brain Region	Hemi	Cluster No.	x	y	z	N Studies (n Foci)	Volume (mm^3)	Contributing studies
Supplementary motor area, dorsal Anterior Cingulate	L	1	-4	22	44	4 (5)	992	Westbrook et al, 2019; Bahlmann et al., 2015; Chong et al., 2017; Padmala et al., 2011;
Middle frontal gyrus	L	2	-46	24	26	4 (4)	839	Chong et al., 2017; Leong et al., 2018; Padmala et al., 2010; Padmala et al. 2011