



Neurobiological foundations and clinical relevance of effort-based decision-making

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Abstract

Applying effort-based decision-making tasks provides insights into specific variables influencing choice behaviors. The current review summarizes the structural and functional neuroanatomy of effort-based decision-making. Across 39 examined studies, the review highlights the ventromedial prefrontal cortex in forming reward-based predictions, the ventral striatum encoding expected subjective values driven by reward size, the dorsal anterior cingulate cortex for monitoring choices to maximize rewards, and specific motor areas preparing for effort expenditure. Neuromodulation techniques, along with shifting environmental and internal states, are promising novel treatment interventions for altering neural alterations underlying decision-making. Our review further articulates the translational promise of this construct into the development, maintenance and treatment of psychiatric conditions, particularly those characterized by reward-, effort- and valuation-related deficits.

Keywords Effort-based decision-making · Valuation · Effort · Reward · Neural correlates · Imaging

Introduction

Effort-based decision-making (EBDM) encompasses mental computations that estimate work (“effort”) amounts required for a positive outcome (“reward”) Kurniawan et al., 2010; Prévost et al., 2010; Treadway et al., 2009. Applying a neuroeconomic lens to assess decision-making can be valuable in operationalizing and quantifying

motivation and further parsing it into its basic elements Chong et al., 2016; this framework can develop mechanistic theories, computational models and testable approaches to understand choice behavior Chong et al., 2016; Pessiglione et al., 2018. This approach separates the two components that make up effort-based decision-making – namely *effort* (the motivational aspects of decision-making) and *reward* (including reward responsiveness). While traditional models of effort focus primarily on discounting and costs, practical models can subdivide *costs* into various components including *effort expenditure* (i.e. work – the amount of energy/time put into obtaining rewards), *risk-taking* (engaging in behaviors under conditions of threat or uncertainty to obtain a reward), and *reward discounting* (i.e. temporal costs with the devaluing of reward over time or opportunity costs) Chong et al., 2016; Zald & Treadway, 2017. Participants may not know how much effort is needed to obtain a reward, and thus a probabilistic element is evident as participants may expend considerable amounts of effort without attaining a reward. The reward element encompasses constructs of anticipation, consumption, type, magnitude and the state of the individual (e.g. mood or energy levels) Berridge & Robinson, 1998;

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Chong et al., 2016; Knutson et al., 2004. Indeed, EBDM fits into the Positive Valence Domain of the Research Domain Criterion (RDoC) framework launched by the National Institute of Mental Health (NIMH) (<https://www.nimh.nih.gov/research/research-funded-by-nimh/rdoc/constructs/rdoc-matrix.shtml>), which includes a *reward valuation* construct, made up of *reward probability*, *delay* and *effort* subconstructs, suggesting that alterations in the way a reinforcer is computed as a function of its magnitude, valence, predictability, the time interval prior to its expected delivery, and the perceived costs of the physical or cognitive effort required to obtain it may be shared across psychiatric disorders.

The application of EBDM tasks has provided behavioural insights into specific variables influencing choice behaviours, particularly when choice-relevant information is not always available. In particular, behavioural assessments of EBDM, including tasks that measure various EBDM constructs of Brand et al. (2005); Bechara et al., 1994; Lejuez et al., 2002; Madden & Bickel, 2010; Odum, 2011; Rachlin & Green, 1972; Knutson et al., 2000; Hodos, 1961; Kool et al., 2010; Horan et al., 2015, have identified subjective valuation, effort valuation, reward magnitude, choice difficulty and choice probability as contributing to reward-, effort- and valuation-related impairments (see Box 1) Hélie et al., 2017; Rangel et al., 2008. Importantly, details of particular EBDM tasks can vary widely, and these details may be crucial in precipitating the pattern of individual performance differences or the corresponding neural substrates. Key details include hypothetical versus experiential aspects, probabilistic features, the output type, the nature of the reward, the motivational state of the individual, and the task duration. Further, expectancies about how much effort is needed, and how precisely the expected effort cost is calculated may vary widely from paradigm to paradigm depending on how the paradigm is arranged, and additionally varies across age (i.e., adolescents compared to adults) Rodman et al., 2021. Nevertheless, impairments in reward-, effort- and valuation-related processes are increasingly reported across psychiatric conditions Addicott et al., 2020; Brassard & Balodis, 2021; Chang et al., 2019; Cooper et al., 2019; Culbreth et al., 2018, 2020; Damiano et al., 2012; Docx et al., 2015; Fervaha et al., 2015; Green & Horan, 2015; Hartmann et al., 2015; Mansur et al., 2019; Mata et al., 2017; Mitchell & Sevigny-Resetco, 2020; Mosner et al., 2017; Racine et al., 2019; Taylor & Filbey, 2021; Treadway et al., 2009, 2012, 2015; Yang et al., 2014.

Box 1 Effort-Based Decision-Making Constructs and Descriptions

Subjective Valuation	The within-individual variability in preferences for rewards and/or actions. The process of assigning values/weights to different options based on a person's current state (Hélie et al., 2017; Slovic, 1995; Slovic et al., 1977). Subjective valuation is usually produced from a subjective rating that is used to compare the desirability of different options (i.e., predicting the benefits associated with each possible choice) (Hélie et al., 2017; Rangel et al., 2008). Typically, when choosing between multiple options, decision-makers will select or prefer options with the highest subjective value (i.e., the options with the most value relative to other choices)
Effort Valuation	The within-individual variability in the mental calculations performed to determine cost/effort required to obtain rewards. Like subjective valuation, effort valuations are context-dependent and change relative to the decision-makers environment, states and other available options. Typically, when choosing between multiple options, decision-makers will select or prefer options requiring the least amount of effort (i.e., an easy task over a hard task)
Reward Magnitude	The size or number of benefits associated with chosen options (i.e., size/portion of food rewards or the amount of monetary rewards). Larger reward magnitudes are normally perceived more favorably when compared to smaller reward options. Typically, decision-makers assign greater values to choices/options leading to larger benefits (Rangel et al., 2008)
Choice Difficulty	The degree of physical or cognitive demand associated with each task trial (i.e., hard tasks versus easy tasks). Several key factors contribute to the valuation of choice difficulty, including individual differences, cognitive load, time, effort costs and reward magnitude (Bonnelle et al., 2015; Hogan et al., 2019). In this latter sense, cost-benefit weighing becomes more difficult as benefits and costs become of similar magnitudes (Bonnelle et al., 2015)

Choice Probability	The likelihood that a certain task results in reward receipt. Choice probability influences valuation processes, as decision-making often requires assessing rewards and costs that occur probabilistically (i.e., prospects) (Rangel et al., 2008). Probabilities can be explicitly shown to participants in decision-making tasks (e.g., GDT and EEfRT task) or intentionally withheld requiring participants to draw on past experiences and learn as the task progresses (e.g., Deck Choice Effort Task and IGT)	Prediction Error/Expectation violation	The discrepancy between an individual's anticipated outcome or reward and the actual outcome or reward received after expending effort on a particular task or activity. Prediction effort/expectation violations reflect the difference between what a person expected to gain from their efforts and what they actually obtained. This construct is crucial in understanding updating mechanisms (i.e., adjusting decision-making strategies)
Reward Valuation	The within-individual variability in preferences for rewards. Similar to subjective valuation, reward valuation is the act of attributing values or significance to incentives. Incentives that carry greater value or are perceived as more gratifying tend to result in enhanced performance (i.e., individuals will exert greater effort in pursuit of higher-valued rewards) (Arulpragasam et al., 2018)	Reward-Effort Integration	The point in an effort-based decision-making where information about prospective effort expenditure and potential reward outcomes are combined to guide decision cost/benefit computations
Effort Anticipation/Effort Prospect	Closely related to effort valuation, effort anticipation (also referred to as effort prospect/prospective effort) refers to the process through which individuals consider the expected amount of physical, mental, or emotional effort required to obtain a reward. It involves estimating the difficulty and strenuousness of the effort before deciding whether to pursue the task		
Reward Anticipation	Similar to effort anticipation, reward anticipation refers to the process through which individuals consider the expected size and receipt of a reward. In other words, reward anticipation focuses on the assessment of potential rewards		
Effort Expenditure	The actual allocation or utilization of physical, cognitive, or emotional resources to complete a specific task or activity. This is a tangible construct, referring to the effort exerted by an individual to achieve a reward		

In addition to behavioural assessments, prior neuroimaging studies have identified the ventromedial prefrontal cortex (vmPFC), the dorsal anterior cingulate cortex (dACC), the ventral striatum (VS), the posterior cingulate cortex (PCC), the amygdala, and the insula contributing to EBDM processes Kable & Glimcher, 2009; Prévost et al., 2010. Specifically, the vmPFC has been shown to play a role in subjective valuation of both primary and secondary rewards Bartra et al., 2013; Chib et al., 2009; Clithero & Rangel, 2014; Kim et al., 2011; Lin et al., 2012; O'Doherty, 2011, 2014. In the absence of reward, BOLD signals reveal that the vmPFC encodes the subjective valuation of prospective effort Hogan et al., 2019 and is also recruited in experienced utility signals and prediction errors, suggesting shared anatomical substrates involved in decision-making processes Arulpragasam et al., 2018; Lin et al., 2012. The integration of effort and reward information during decision-making also recruits the vmPFC, in addition to the dACC, supplementary motor area (SMA), insular cortices and VS to form a distinct neural network Arulpragasam et al., 2018; Bartra et al., 2013; Klein-Flugge et al., 2016; Levy & Glimcher, 2012. When effort and reward cues are presented simultaneously, the dACC, putamen and the anterior insula (aI) engage simultaneously Arulpragasam et al., 2018. Preclinical models additionally support the role of the medial PFC and ACC during

effort valuation and effort expenditure for rewards Fatahi et al., 2020; Rudebeck et al., 2006, and demonstrate neural synchronization between brain regions during decision-making Fatahi et al., 2020. Indeed, a recent meta-analysis of functional magnetic resonance imaging studies assessing the neural basis of effort valuation specifically in humans additionally suggests that the pre-SMA scales positively with effort demands, whereas vmPFC activation is involved in signaling net values, thus providing strong evidence for different, yet complementary, roles of the vmPFC and pre-SMA in valuing effort costs, and as two core regions of a network that drive motivated behavior Lopez-Gamundi et al., 2021. Additionally, the cingulate, particularly more anterior areas, is linked to signaling trade-offs between competing options (i.e., more difficult choices may involve selecting between options with similar costs and benefits) and likelihood or probability that an individual will select a particular option amongst alternatives respectively Bonnelle et al., 2015; Hogan et al., 2019; Huang et al., 2016. Thus, this body of work collectively suggests that brain regions involved in subjective valuation, effort valuation, reward magnitude, choice difficulty and choice probability, may have unique, yet overlapping functions. However, given the potential impact of methodological limitations in prior studies, including variations in employed EBDM tasks, imaging techniques, psychiatric populations, and variables of interest, conducting a systematic review on the topic is imperative. This approach promises to unveil significant patterns and trends in this rapidly expanding field.

The effort expenditure for rewards task

Based on a translational measure of reward motivation Salamone et al., 1994, the Effort Expenditure for Rewards Task (EEfRT) was developed to behaviorally assess components of effort expenditure, reward magnitude and reinforcement schedules in humans Treadway et al., 2009. The EEfRT presents individuals with a choice of ‘easy-tasks’ (30 button presses within 7 s using the dominant index finger) or ‘hard-tasks’ (100 button presses in 21 s using the non-dominant little finger) associated with varying monetary rewards Treadway et al., 2009. By separating reward probability, reward magnitude, and effort expenditure (often confounded in other neuropsychological tasks) the EEfRT behaviorally quantifies aspects of motivation and captures individual differences in effort-expenditure for rewards Treadway et al., 2012. Although other neuropsychological tasks assess various EBDM constructs, the EEfRT is currently the only behavioural task recommended to assess effort valuation in the revised RDoC matrix.

A scanner-adapted EEfRT task has participants choose between ‘no-effort tasks’ for \$1.00 or ‘high-effort’ tasks for larger rewards. Effort expenditure consists of

repeated button-presses to raise the height of a vertical bar (20%/50%/80%/100%). Each trial sequentially presents reward or effort information at 2 cue-points, followed by a Decision Prompt, and Choice phase Arulpragasam et al., 2018. By temporally disconnecting effort expenditure and reward magnitude, the EEfRT fMRI version permits investigation of how these constructs independently and simultaneously influence effortful goal-directed choice behavior Arulpragasam et al., 2018. With an increasing number of studies employing the scanner-adapted version of the EEfRT, a review of recent neuroimaging findings utilizing this task relative to other EBDM tasks is timely.

Clinical applications

Importantly, clinical applications of EBDM paradigms are also gaining interest Wolpe et al., 2024. For instance, one behavioural study demonstrated that the EEfRT is the most promising paradigm to detect group differences and treatment outcomes in individuals with schizophrenia Reddy et al., 2015. Importantly, promising applications of EBDM tasks have also been shown in depression, generalized anxiety disorder, and attention deficit/hyperactivity disorder and schizophrenia [for review see Wolpe et al. 2024]. Other cost related tasks also relate to intervention responses Elton et al., 2019 but are beyond the scope of the current review. While the clinical applications of EBDM studies underscore its potential for targeted therapeutic interventions in shifting reward-based expectations, the neurobiological properties underlying clinically relevant changes has yet to be elaborated.

Current review

Considering the increasing number of EBDM studies, a review of the neurobiological research is timely. One recent meta-analysis has begun to shed light in this direction by quantitatively synthesizing fMRI data to identify neural correlates specific to effort-related cost processing and value integration in healthy adults Lopez-Gamundi et al., 2021. However, given the variations in employed EBDM tasks, imaging techniques, psychiatric populations, and variables of interest, a further review accounting for these factors can additionally identify neurobiological trends in EBDM studies. Thus, the current systematic review first and foremost extends findings from the prior meta-analysis by including multiple neuroimaging approaches and conducting a qualitative synthesis of these studies examining the spectrum of EBDM constructs, across healthy controls and psychiatric disorders, in order to 1) fully understand the scope of neural processes underlying cost–benefit computations and 2) understand how these neural processes may

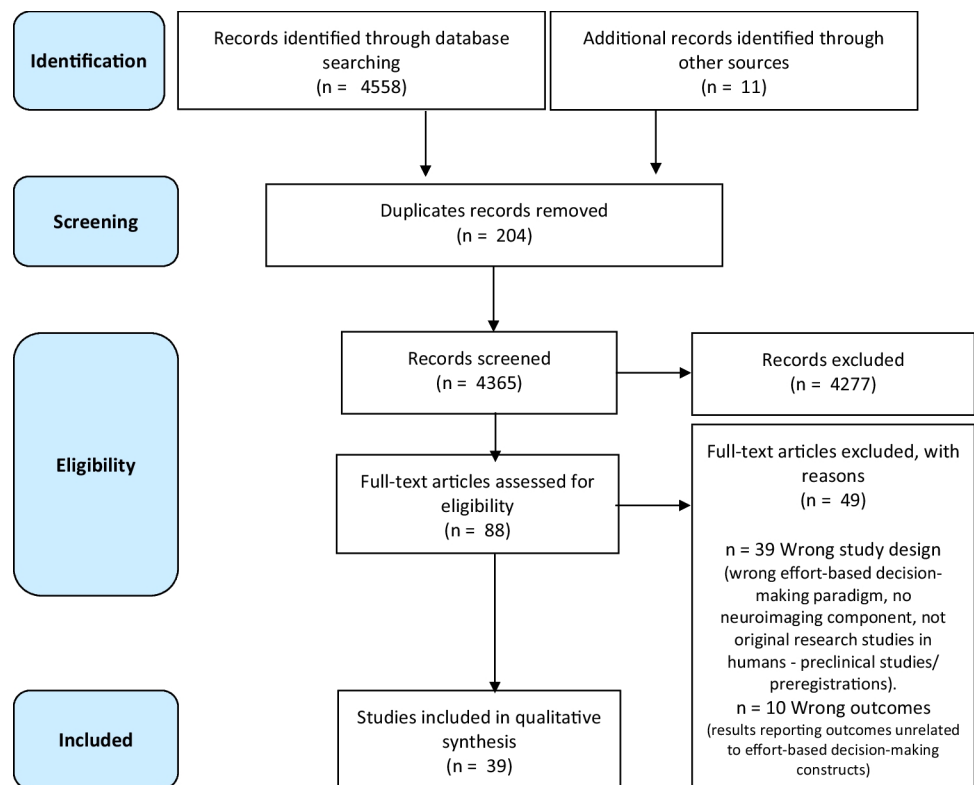
manifest in psychiatric populations. Second, we provide a novel translational aspect in our review to explore how effort-based neurobiological mechanisms relate to treatment outcomes across psychiatric populations. More specifically, the focus of the current review is to summarize the literature examining the underlying structural and functional anatomy of EBDM components, and subsequently discuss ways in which this framework can be applied to interventions for disorders characterized by reward-, effort- and valuation-related deficits.

Methods

A systematic literature review using PRISMA guidelines was conducted on PubMed, Web of Science and PSY-CINFO for studies investigating the neural correlates of EBDM. Searches included keywords “decision-making” and “effort-based decision-making” coupled with “neuropsychology”, “neuroscience”, and “imaging”. The Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines were followed (see Fig. 1) (Moher et al., 2009). Database searches were conducted through October 2022 and were not restricted by year or journal (except for English language). The

returned records were uploaded to Covidencetm, an online software used to help streamline the systematic review process. Our searches generated 4558 articles; title and abstracts were independently reviewed by SB and HL to ensure relevance. Eleven additional resources were identified through other sources, including recommendations made during peer-review. To be included, studies had to meet the following criteria: 1) published in an English language peer-reviewed journal, 2) reflect original research in human participants (i.e. commentaries, abstracts, meta-analyses and systematic reviews were excluded), 3) include at least one neuropsychological task assessing EBDM and its constructs (i.e., studies employing any EBDM task that assesses subjective valuation, effort valuation, reward magnitude, choice difficulty and choice probability) and included at least one form of neuroimaging (i.e. fMRI, PET, EEG) and 4) include either a comparison psychiatric group with a control group OR a correlation coefficient measuring the association between neural functioning during effort-based choices and the experimental group of interest. Of these, 4530 studies were excluded after screening out duplicates and studies not meeting our inclusion criteria. A total of 39 studies met criteria for inclusion in our review.

Fig. 1 Preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow diagram



Results

Thirty-nine studies met inclusion criteria; Table 1 presents EEfRT and EEfRT-variation study results ($N = 20$, EEfRT-variation studies resemble the traditional EEfRT task with slight modifications, thus not identical to the original EEfRT task); Table 2 presents study results from studies assessing EBDM constructs of interest by using alternative EBDM tasks including approach-avoidance conflict tasks, cue-predictive instrumental task, delay and effort discounting choice task, risk taking tasks and modified monetary incentive delay tasks ($N = 19$). While these tasks do not comprehensively fit with the main effort-based decision-making criteria, these alternative EBDM studies were included in our review as results emphasized patterns of neural functioning and influences relevant to our predetermined EBDM constructs of interest. Neuroimaging techniques adopted in EEfRT and EEfRT-variation studies specifically included fMRI Aridan et al., 2019; Arulpragasam et al., 2018; Bernacer et al., 2019a; Bonnelle et al., 2015; Croxson et al., 2009; Culbreth et al., 2020; Hogan et al., 2019, 2020; Huang et al., 2016; Klein-Flugge et al., 2016; Kurniawan et al., 2010; Nagase et al., 2018; Suzuki et al., 2021; structural magnetic resonance imaging (sMRI) Mathar et al., 2016; Umesh et al., 2020; electroencephalography (EEG) (Giustiniani et al., 2020; Harris & Lim, 2016; cTBS stimulation Soutschek & Tobler, 2020; diffusion weight MRI Saleh et al., 2021 and a combined fMRI and sMRI technique Yang et al., 2016. Study populations included healthy individuals Aridan et al., 2019; Arulpragasam et al., 2018; Bernacer et al., 2019a, 2019b; Bonnelle et al., 2015; Croxson et al., 2009; Giustiniani et al., 2020; Harris & Lim, 2016; Hogan et al., 2019, 2020; Klein-Flugge et al., 2016; Kurniawan et al., 2010; Nagase et al., 2018; Soutschek & Tobler, 2020; Suzuki et al., 2021; Umesh et al., 2020; schizophrenia Culbreth et al., 2020; Huang et al., 2016; obesity Mathar et al., 2016; small vessel cerebrovascular disease (SVD) Saleh et al., 2021 and individuals with first-episode major depressive disorder (MDD) Yang et al., 2016. Combined across EEfRT and EEfRT-variation studies, a total of 753 participants (42% female) completed a neuroimaging protocol, 566 of which were healthy controls (43% female). Healthy controls across EEfRT and EEfRT-variation studies were right-handed, had normal or corrected-to-normal vision, no history of psychiatric or neurological diseases, and had no structural brain abnormalities Aridan et al., 2019; Arulpragasam et al., 2018; Bernacer et al., 2019a, 2019b; Bonnelle et al., 2015; Croxson et al., 2009; Giustiniani et al., 2020; Harris & Lim, 2016; Hogan et al., 2019, 2020; Klein-Flugge et al., 2016; Kurniawan et al., 2010; Nagase et al., 2018; Soutschek & Tobler, 2020; Suzuki et al., 2021; Umesh et al., 2020. For the purpose of this review, only results from studies including

healthy adults are discussed in-text. A more detailed reporting of all study results, including clinical populations, are included in Tables 1 & 2.

Identified effort-based decision-making constructs

Studies using the EEfRT task specifically assessed subjective valuation Arulpragasam et al., 2018; Klein-Flugge et al., 2016, effort valuation Arulpragasam et al., 2018; Hogan et al., 2019, 2020, reward magnitude Arulpragasam et al., 2018; Giustiniani et al., 2020; Huang et al., 2016; Klein-Flugge et al., 2016; Suzuki et al., 2021, choice difficulty Hogan et al., 2019, 2020, choice probability Huang et al., 2016, reward valuation Arulpragasam et al., 2018, effort anticipation/effort prospect Arulpragasam et al., 2018; Suzuki et al., 2021, reward anticipation Arulpragasam et al., 2018; Giustiniani et al., 2020, effort expenditure Huang et al., 2016; Mathar et al., 2016; Suzuki et al., 2021, prediction error/expectation violation Arulpragasam et al., 2018, and reward-effort integration Arulpragasam et al., 2018; Klein-Flugge et al., 2016; Suzuki et al., 2021 (for construct descriptions, see bottom half of Box 1).

Patterns of neural activation associated with effort-based decision-making constructs

Subjective valuation

In EEfRT fMRI studies specifically examining subjective valuation, one identified vmPFC recruitment Arulpragasam et al., 2018; 2 reported dACC (decreased activation Arulpragasam et al., 2018; increased activation Klein-Flugge et al., 2016; and one study found pre-SMA activity encoding positive difference in SV between chosen and unchosen options Klein-Flugge et al., 2016 (see Fig. 2a). In EEfRT-variation MRI studies, one identified pre-SMA, motor cortex, cingulate motor area and VS activity related to high cost–benefit value (high reward discounted by effort) Croxson et al., 2009, and one identified posterior cingulate recruitment related to subjective value in consistent decisions Bernacer et al., 2019b. One EEfRT-variation EEG study found increased vmPFC, dmPFC, precuneus and posterior parietal cortex amplitudes related to net values (i.e., subjective value – effort cost) Harris & Lim, 2016. In alternative EBDM fMRI studies, one identified VS activation Westbrook et al., 2019 and a second specified dACC, dIPFC, inferior frontal sulcus, intraparietal sulcus, SPL, IPL, and aI activity related to cognitive effort, and dACC, dmPFC, dIPFC, intraparietal sulcus activation to physical effort Chong et al., 2017. Importantly, one alternative EBDM fMRI found no significant VS and vmPFC activation during subjective valuation of either cognitive or physical effort Chong et al., 2017.

Table 1 Underlying neurocircuitry of effort-based decision-making using an Effort Expenditure for Rewards Task

Task	Authors & Imaging Methodology	Group & Demographics	Variable of Interest	Neuroimaging Results
Effort Expenditure for Rewards Task	Arulpragasam et al., 2018	HC	Subjective Valuation:	↑ vmPFC activity, ↓ dACC activity, no VS.
	Computational fMRI	N=28 (15F) Mean age 20.8 (SD 3.4)	Effort Valuation: Reward Value:	No significant clusters ↑ vmPFC activity, ↓ dACC activity, no VS.
	WB & ROI (dACC, Insula, caudate)		Expectation Violation: Reward Anticipation: Reward Magnitude:	↑ insula activity when cue 1 is large reward followed by cue 2 high effort. ↑ vmPFC activity when reward information is first presented No significant clusters.
	Klein-Flügge et al., 2016	HC	Reward-Effort Integration: Reward-Effort Integration:	VS involved in cost/benefit integration. Putamen integrates effort and reward information for all Cue 2 trials SMA and dACC integrating information from reward and effort cues during decision phas
fMRI	WB & ROI (putamen, SMA, vmPFC)	N=21 (11F) Mean age 28 Age range 19–38	Subjective Valuation: Reward Magnitude: Effort Expenditure:	SMA, dACC, and putamen: encodes positive difference in SV between chosen and unchosen options. vmPFC encodes reward magnitudes. No significant correlations between BOLD signals and reward weight. SMA and putamen encoded effort weight more strongly on choices negatively influenced by high effort.
	Suzuki et al., 2021	HC	Effort Anticipation:	↑ dorsal VS related to anticipation of effortful movement . No signals in dorsomedial subregion of the striatum (dmS).
fMRI	WB & ROI (dmS, anterior VS, putamen)	N=29 (21F) Mean age 24.41 (SD 5.43)	Effort Expenditure:	↑ dorsal VS related to initiation of effortful movement . dmS activity sensitive to effort activation .
	Huang et al., 2016	Schizophrenia: N=23 (3F) Mean age 34.48	Reward Magnitude: Reward-Effort Integration: Reward Magnitude:	↑ putamen activity related to 'simple' movement initiation . Anterior VS encodes magnitude of reward . VS sensitive to discounted reward values by effort (response to reward was significantly lower after effort.) ↓ NAcc, caudate, posterior cingulate, and medial frontal gyrus activation in SCZ, relative to HC group. SCZ Nacc signal did not scale to reward magnitude.
fMRI			Choice Probability:	NAcc, cingulate and medial frontal gyrus signal with prob-ability. - Neural responses HC>SCZ participants

Table 1 (continued)

Task	Authors & Imaging Methodology	Group & Demographics	Variable of Interest	Neuroimaging Results
	WB & ROI (vmPFC)	HC: N=23 (8F) Mean age 34.91 Obese: N=29 (14F) BMI: 30-40.	Effort Expenditure:	↑ NAcc activation related to ↑ willingness to expend high-level effort.
	Mathar et al., 2016	HC: N=28 (15F) BMI: 19-25	Effort Expenditure:	No association of NAcc volume and subjects' willingness to exert effort.
	sMRI			
	WB & ROI (NAcc)	Age range 18-35		
	Giustiniani et al., 2020	HC	Reward Magnitude:	↑ vmPFC amplitude following a reward vs. absence of reward.
		N=28 (0F)	Reward Anticipation:	No significant signals when waiting for reward after easy and hard tasks.
	EEG	Mean age 25 (SD 5.29)		
Effort Expenditure for Rewards Task Variation	Aridan et al., 2019	HC	Effort Anticipation/Prospect:	↑ L primary sensory cortex activation related to ↑ prospective effort .
	fMRI	N=40 (21F)	Effort Expenditure:	↑ vmPFC activity related to decreasing physical demand . ↑ L sensorimotor cortex & L superior parietal lobule activation related to ↑ prospective risk .
	WB	Mean age 22.62 (SD 2.90)		↓ MFC, ACC, PCC, R striatum, frontal polar cortex and R sensorimotor cortex activity related to ↑ prospective risk .
	Bernaer et al., 2019a	HC	Prediction Error/Expectation Violation:	↑ PCC, dACC, pre-SMA activation related to behavioural inconsistency .
	fMRI	N=24 (14F)	Subjective Valuation:	↑ PCC activity related to subjective value in consistent decisions .
	ROI (vmPFC, dmPFC, Nacc, anterior cingulate, PPC, Insula, amygdala, putamen)	Mean age 19.8 Age: 18-25	Effort Expenditure:	↑ L NAcc & cingulate cortex activity related to No-risk/No-effort > No-risk Maximum-effort decisions .
	Bonnelle et al., 2015	HC	Reward Expectancy:	↑ activation in the caudate, CMA and SMA related to reward expectancy . ↓ basal ganglia activity related to effort valuation .
	fMRI DTI	N=37 (20F) Mean age 26 (SD 4.4) Age range 19-38	Effort Valuation & Anticipation:	R vIPFC implicated in stake evaluations .

Table 1 (continued)

Task	Authors & Imaging Methodology	Group & Demographics	Variable of Interest	Neuroimaging Results
	WB & ROI (pre-SMA, SMA, M1, dACC, CMA)		Choice Probability:	↑ dACC & pre-SMA, and ↓ vmPFC activity related to cost-benefit weighing
	Crosson et al., 2009*	HC N=19 (10F)	Subjective Valuation:	↑ SMA, CMA & M1 activity related to choice probability (anticipation of an effortful motor response) . ↑ VS and midbrain activity to high cost-benefit value (high reward discounted by effort).
	fMRI		Reward Expectation:	↑ activation in premotor and motor regions, SMA and CMA related to cost-benefit value .
	ROI (dACC, VS, dopaminergic midbrain, posterior OFC, insula)	Age range 19–27	Effort Anticipation/Prospect:	Increased reward expectation related to ↑ dACC activation, anterior insula and posterior OFC. Increased effort expectation related to ↓ dACC activation and ↑ Putamen activation.
	Hogan et al., 2019	HC	Effort Valuation:	↑ vmPFC activity: during effort choices, increases as relative value for certain option increased. - subjective utility of effort value is inversely associated with vmPFC activity
	fMRI	N=34 (15F)		
	WB & ROI (vmPFC and ACC)	Mean age 23 Age range 18–34	Choice Difficulty:	No signals in ACC. ↑ ACC activation related to increased choice difficulty
	Hogan et al., 2020	HC	Effort Valuation:	↑ dACC and bilateral insula activation related to chosen effort values during choice phase. Activity occurred for both baseline and fatigue choice phases.
	fMRI	N=20 (9F)		↑ R insula activity related to changes in effort value resulting from fatigue (insensitive to effort values in rested state). ↓ L premotor and M1 cortical activation during choice phase in a fatigued state.
	WB & ROI (Insula, ACC, premotor cortex)	Mean age 24 (range 18–34)		
	Kurniawan et al., 2010	HC	Effort Magnitude:	Activity in the anterior part of right superior frontal gyrus related to grip choices (effortful task).
	fMRI	N=18 (5F)		↑ activation in putamen related to choosing low effort grip option . (signals effort information with ↓ effort resulting in ↑ activation).
	WB	Mean age 27		↑ activation left motor cortex, right cingulate motor area, and right supplementary motor area also related to low effort grip options .
	Nagase et al., 2018	HC	Effort Anticipation/Prospect:	dmFC, dACC and right anterior middle frontal gyrus positively correlated with expected costs of chosen option . vmPFC negatively correlated with expected costs of chosen option .
	fMRI	Experiment 1: N=33 (4F)		
	WB	Mean age 25.5 (SD 5.4).		

Table 1 (continued)

Task	Authors & Imaging Methodology	Group & Demographics	Variable of Interest	Neuroimaging Results
	Umesh et al., 2020	Experiment 2: N=20 (2F) Mean age 24.7 (SD 6.2) HC	Effort Valuation:	↑ hand knob cortical thickness associated with higher subjective cost of effort in decisions.
sMRI	ROI (R & L precentral gyrus – hand knob region)	N=24 (12F) Mean age 23.13 Age range 18–34		
	Harris & Lim, 2016 EEG	HC N=25 (8F)	Subjective Valuation:	↑ amplitude in the vmPFC related to net value (subjective value – effort cost).
	ROI (dmPFC, vIPFC, IPS, premotor & motor cortex)	Ages 18–40	Effort Expenditure:	Effort costs – ↑ amplitude in the middle cingulate, somatosensory, motor/premotor cortices (100–250ms after stimulus). Value – ↑ amplitude in the dmPFC, precuneus, PPC (400ms before response). ↓ RTs following cTBS of the dlPFC compared with control areas.
	Soutschek & Tobler, 2020	HC		
cTBS (dlPFC)		N=60 (29F) Mean age 23.7 (SD 2.7)		dlPFC stimulation decreases fatigue after effort exertion dlPFC disruption ↑ effort discounting before effort accumulation.
	Culbreth et al., 2020 fMRI	Schizophrenia: N=28 (8F) Mean age 37.18 (SD 12.25)	Effort Expenditure:	↑ activation in posterior parietal/occipital cortex, middle cingulate cortex, PCC, left postcentral gyrus, and left precuneus during hard task across participants.
	WB & ROI (VS, cerebellar, frontal, cingulate, parietal and insular cortices)	HC: N=30 (7F) Mean age 35.2 (SD 10.63)	Choice Difficulty:	No differences in WB analysis between SCZ and HC groups in hard > easy contrast .
	Saleh et al., 2021	Small vessel cerebrovascular disease		↓ white matter integrity in dACC, vmPFC, and NAcc related to apathy, not depression.
	Diffusion weighted MRI	N=82 (37F) Mean age 68 (SD 11). N=62 scans		Drift rate influenced by white matter integrity in the apathy network (dACC, vmPFC and NAcc).
	Yang et al., 2016	MDD: N=25 (13F)	Choice Probability:	MDD: ↓ activation in R caudate and L middle temporal gyrus for high-reward during high probability trials.

Table 1 (continued)

Task	Authors & Imaging Methodology	Group & Demographics	Variable of Interest	Neuroimaging Results
	fMRI and sMRI WB & ROI (R & L caudate, L superior temporal gyrus)	Mean age 28.96 (SD 7.00) HC: N=25 (15F) Mean age 28.36 (SD 7.87)	Reward Magnitude:	<p>↓ activation in R caudate and lSTG for high-probability trials.</p> <p>↓ activation in superior temporal gyrus activity related to hard tasks with high probability.</p> <p>HC: ↓ activation in R caudate related to hard tasks with high probability</p>

WB = whole brain; ROI = region of interest; fMRI = functional magnetic resonance imaging; sMRI = structural magnetic resonance imaging; EEG = electroencephalogram; DTI = diffusion tensor imaging; cTBS = continuous theta burst stimulation; HC = healthy controls; MDD = major depressive disorder; SCZ = schizophrenia; F = female; SD = standard deviation; vmPFC = ventromedial prefrontal cortex; vlPFC = ventrolateral prefrontal cortex; dmPFC = dorsomedial prefrontal cortex; MFC = medial frontal cortex; OFC = orbitofrontal cortex; VS = ventral striatum; dmS = dorsomedial striatum; NAcc = nucleus accumbens; dACC = dorsal anterior cingulate cortex; SMA = supplementary motor areas; M1 = primary motor cortex; CMA = cingulate motor area; PCC = posterior cingulate cortex; PPC = posterior parietal cortex; IPS = intraparietal sulcus; R = right; L = left, BOLD = blood-oxygen-level-dependent imaging; SV = subjective value; RT = reaction time

* Croxson et al. (2009): neuropsychological task does not include an element of choice

Effort valuation

In EEfRT fMRI studies during effort valuation, one study showed no significant activity differences Arulpragasam et al., 2018 (see Fig. 2b). One EEfRT-variation fMRI study demonstrated increased vmPFC activation as the relative value for certain option increased Hogan et al., 2019, one identified increased dACC and bilateral insula activation related to chosen effort values during choice phase Hogan et al., 2020, one identified cingulate motor areas and basal ganglia activation related to effort valuation Bonnelle et al., 2015 and one EEfRT-variation sMRI study demonstrated increased cortical thickness in motor cortex areas associated with higher subjective cost of effort in decisions Umesh et al., 2020. One alternative EBDM fMRI study identified increasing ACC/insula activity with larger effort Prévost et al., 2010.

Reward magnitude

In EEfRT fMRI studies, two reported greater vmPFC activation Giustiniani et al., 2020; Klein-Flugge et al., 2016, one demonstrated increased anterior VS activity Suzuki et al., 2021, one demonstrated nucleus accumbens, caudate, PCC, and medial frontal gyrus activity Huang et al., 2016 and one found no significant clusters of activation Arulpragasam et al., 2018 when viewing reward magnitudes (see Fig. 2c). One EEfRT EEG study demonstrated increased vmPFC amplitudes following a reward vs. absence of reward Giustiniani et al., 2020. One alternative EBDM fMRI study found increased vmPFC and VS activation related to increasing rewards Westbrook et al., 2019. A second alternative EBDM fMRI study found increased ACC, superior parietal lobe, aI, posterior OFC, frontal eye field, fusiform gyrus, dIPFC, mid-brain/substantia nigra, striatum and inferior parietal cortex activity for high relative to low reward targets Stoppel et al., 2011. One alternative EBDM EEG study identified increased event-related potentials (ERPs) following gains versus losses Bogdanov et al., 2022 while a second EEG study demonstrated gains eliciting significant RewP amplitudes relative to losses Bowyer et al., 2021.

Choice difficulty

No study using the EEfRT assessed choice difficulty. One EEfRT-variation fMRI study identified greater ACC activation with increased choice difficulty Hogan et al., 2019 (see Fig. 2d). One alternative EBDM fMRI study identified greater pre-SMA and dACC activation related to decision difficulty Westbrook et al., 2019. A second alternative EBDM fMRI study identified no significant clusters of activation signaling choice difficulty Chong et al., 2017.

Table 2 Underlying neurocircuitry of effort-based decision-making using an alternative decision-making task

Authors & Imaging Methodology	Group & Demographics	Task	Variable of Interest	Neuroimaging Results
Abivardi et al., 2020 fMRI ROIs (anterior hippocampus, anterior dentate gyrus, amygdala)	HC N=20 (11F) Mean age 23.10 (SD 3.34)	Approach-Avoidance Conflict Task (AAC Task)	Choice Probability:	<p>↑ activation in left anterior hippocampus and entorhinal cortex related to threat probability and magnitude.</p> <p>↑ activation in anterior hippocampus on avoidance trials</p> <p>↑ activation in amygdala on approach trials.</p> <p>L anterior hippocampus responded to high threat probability and R anterior hippocampus activation related to low threat probability.</p> <p>L lateral amygdala responded to low and high, but not intermediate, threat probability.</p>
Chong et al. 2017 fMRI WB and ROIs (VS, vmPFC, paracinate gyrus, subcallosal cortex, frontopolar cortex, dorsal PCC, left OFC, NAcc)	HC N=34 (23F) Mean age 24 Age range 19-39	Combined Cognitive and Physical Effort Task	SV of Cognitive Effort SV of Physical Effort: Domain-general SV: Choice difficulty: Perceived Risk:	<p>↑ activation in the dACC, dlPFC, inferior frontal sulcus, intraparietal sulcus, SPL, IPL, and al.</p> <p>- Cognitive effort > physical effort contrast revealed a significant cluster in the right amygdala. No evidence of domain-specific activity of VS or vmPFC.</p> <p>↑ activation in the dACC, dmPFC, dlPFC, intraparietal sulcus.</p> <p>↑ activation in the dACC, dmPFC, dlPFC, intraparietal sulcus.</p> <p>VS and vmPFC not significantly activated.</p> <p>No significant clusters of activation related to SV of cognitive or physical effort signaled choice difficulty.</p> <p>No significant clusters of activation related to SV of cognitive or physical effort signaled perceived risk of effort level.</p>
Kurniawan et al. 2013* fMRI ROIs (ACC, VS, SMA) McGuire & Botvinick, 2010	HC N=19 (8F) Mean age 21.7 HC Experiment 1: N=10 (4F)	Cue- predictive Instrumental Task Task-switching, avoiding same block in future runs	Effort Anticipation/Prospect: Choice difficulty:	<p>↑ activation in ACC, SMA and striatum related to effort anticipation (expected effort) for high effort trials.</p> <p><u>Experiment 1:</u> L PFC positive correlation with avoiding effortful choices, and self-report effort costs. dmFC no relation</p>
fMRI	Age range 18-34			

Table 2 (continued)

Authors & Imaging Methodology	Group & Demographics	Task	Variable of Interest	Neuroimaging Results
ROIs (dACC, LPFC, dmFC)	Experiment 2: N=22 (14F) Age range 18-30 ADHD: N=21 Mean age = 15.1 SD (1.8)	Delay and Effort Discounting Choice Task (DD-ED Task)		Experiment 2: ↑ activation of LPFC in high-avoidance individuals. ADHD: ↑ posterior corpus callosum/PCC activation, and anterior corona radiata/middle frontal gyrus activity during delay choices . ↑ amygdala activity with increasing delay and effort levels . HC: ↑ posterior corpus callosum/PCC activation, and anterior corona radiata/middle frontal gyrus activity during effort choices .
ROIs (VS, LPFC, PPC, PCC, ACC, aI)	Healthy Controls: N=25 Mean age = 15.4 SD (1.7) Age range 12-17			
Müller et al., 2021 fMRI	HC N=39 Mean age = 25.3 (SD = 4.90) Age range 18–40	Physical effort-based decision-making task	Subjective Valuation:	BOLD response in the MFG and the RCZa signal unrecoverable (long-term) fatigue - Leads to a decrease in the value of working, resulting in choices to rest. - No information about SV encoded BOLD response in RCZp signal recoverable (short-term) fatigue - No information about SV encoded Activity in VS and the FP integrated the SV of working with fatigue state.
WB and ROI (VS, dACC pre-SMA – anterior and posterior rostral cingulate zones)				

Table 2 (continued)

Authors & Imaging Methodology	Group & Demographics	Task	Variable of Interest	Neuroimaging Results
Prettyman et al., 2021 fMRI WB and ROI (VS, dACC, vmPFC)	SCZ: N=21 (10F) Mean age = 32.2 (SD = 10.3) Age range 19 - 54 HC: N=23 (9F) Mean age = 36.6 (SD = 7.7) Age range 22-54	Effort Discounting Task	Choice:	<p>↑ VS and dACC activity in HCs while completing any task (hard and easy trials)</p> <p>↓ vmPFC activity during any hard or easy trials.</p> <p>deactivated VS, dACC, bilateral insula, middle frontal gyrus, and occipital cortex across in all participants</p> <p>No areas positively correlated with effort.</p> <p>Positive correlation with VS activation. Did not activate vmPFC or dACC.</p>
Prévost et al., 2010 fMRI ROIs (vmPFC, VS, M1, ACC, aI)	HC N=16 Mean age 23.1 (SD 1.8)	Delay and effort discounting task	Reward Valuation: Subjective Valuation: Subjective Valuation: Reward-Effort Integration:	<p>Bilateral VS, dACC, frontal cortex, occipital cortex, parietal cortex, insula, and thalamus associated with SV. vmPFC had no effect.</p> <p>SV of chosen options activated VS, and had no effects on dACC and vmPFC.</p> <p>↓ VS and vmPFC activity with longer delays</p> <p>- encode increasing SV of delayed rewards</p> <p>↑ L.M1 activity with SV of the high reward/high effort.</p> <p>↑ ACC and insula activity with larger effort</p> <p>- encoding decreasing SV of effortful rewards with larger efforts.</p> <p>↑ activation in striatum when voluntarily choosing high effort, opposite in forced-choice trials.</p> <p>dACC has similar activation pattern (trend-level significance).</p>
Schouppe et al., 2014 fMRI ROIs (VS, dACC)	HC N=22 (20F) Age range 19-25	Flanker task		

Table 2 (continued)

Authors & Imaging Methodology	Group & Demographics	Task	Variable of Interest	Neuroimaging Results
Stoppel et al., 2011* fMRI WB and ROIs (SPL, anterior insula, posterior OFC, FEF, midbrain/SN, striatum)	HC N=18 (8F) Mean age 25.7 (SD 0.7)	Modified version of the Monetary Incentive Delay Task	Anticipated Reward Magnitude (high > low reward cues): Reward Magnitude (high > low target cues):	↑ activation in the SPL, MTG, medial PFC and occipital pole for high vs. low rewarded trials. ↑ activation in the ACC, SPL, aI, posterior OFC, FEF, FG, dlPFC, midbrain/SN, striatum and IPC for high vs. low reward targets.
			Anticipated Task Difficulty (hard > easy cues): Task Difficulty (hard > easy targets):	↑ activation in the SPL, FEF, FG, LG, dmPFC and dlPFC, SMA and occipital pole for hard vs. easy tasks. ↑ activation in the ACC, SPL, aI, posterior OFC, FEF, IPC, midbrain/SN, NAcc, and striatum for hard vs. easy tasks.
			Reward-Effort Integration:	Anticipatory phase (cue presentation): one single activation cluster within left primary visual cortex. Target-presentation: ↑ activation in the SPL, striatum, midbrain/SN and FEF. ↑ activation in the aI, posterior OFC and lateral occipital sulcus for high vs. low reward feedback
			Feedback:	↑ activation in the ACC, aI, posterior OFC, SPL, lateral PFC, and LG for hard vs. easy feedback. one single activation cluster within aI/posterior OFC for rewardXdifficulty interactions
Vorobyev et al., 2015* fMRI	HC N=34 (0F) Age range 18-19	Stoptlight Game – Risk Taking behaviour		↑ activation in anterior and dorsal cingulate, superior parietal cortex, basal ganglia (including the nucleus accumbens), midbrain, thalamus, and hypothalamus related to risky decision-making . ↑ activation of the medial PFC and striatum related to increased cognitive effort to take risks in low risk-takers, and reward anticipation for risky decisions.
				↑ activation of the caudate nucleus related to enhanced reward processing of risk-taking under peer influence.
				ROIs (dmPFC, vmPFC)

Table 2 (continued)

Authors & Imaging Methodology	Group & Demographics	Task	Variable of Interest	Neuroimaging Results
Westbrook et al., 2019	HC N=21 (11F) Mean age 21	Cognitive Effort Discounting Task (COGED)		↑ activation of bilateral vmPFC, VS, PCC, dACC and ACC encode subjective value .
fMRI				↑ activation of the frontoparietal regions (dACC, bilateral IPS, pre-supplementary motor area, dlPFC) related to decision difficulty .
ROIs (vmPFC, dlPFC, dmPFC, VS, aI, PCC, dACC, ACC amygdala, temporal pole, IPS, IPL, ITG, brainstem, superior gyrus)				↑ activation of bilateral vmPFC and VS related to ↑ reward (benefits) , ↓ activation related to ↑ effort .
Bogdanov et al. 2022	HC N=52 (30F) Mean age 22.85 (SD 3.04) Age range 18–31	Doors task Cognitive Effort Discounting Task		More positive ERP following gains vs. losses (main effect reward). More positive RewP in high-effort vs. low-effort trials (main effect effort level). Nonsignificant effort x reward interaction.
EEG				
Bowyer et al. 2021	HC N=40 (30F) Mean age 19.05 Age range 18–22	Effort-Doors Task	Effort Expenditure:	↑ Effort-P3 amplitude following high-effort expenditure vs. low-effort expenditure trials. No significant main effect of effort level on RewP amplitudes.
EEG				↑ feedback-P3 amplitude following low-effort vs. high-effort expenditure. ↑ negative-going SPN on low-effort vs. high-effort trials. Gains elicited significant RewP amplitudes relative to losses.
			Reward Anticipation:	
			Reward Magnitude:	
			Reward-Effort Integration:	Larger RewP amplitude differences between gains and losses during low-effort vs. high-effort condition (trend significance). Larger feedback-P3 amplitude difference between high- and low-effort conditions for gains vs losses (trend significance).
Ma et al. 2014*	HC N=17 (0F) Mean age 22.59 (SD 1.66)	Cognitive Mental Math Task	Effort Expenditure: Reward-Effort Integration:	High effort Cz, CPz and Pz amplitudes > low effort condition. FRN ↑ negative during neutral feedback vs. positive feedback in the high effort condition. No differences in low effort condition.
EEG				

Table 2 (continued)

Authors & Imaging Methodology	Group & Demographics	Task	Variable of Interest	Neuroimaging Results
ROIs (parietal and frontal electrode sites)				P300 ↑ positive during positive feedback vs. neutral feedback in the high effort condition. No differences in low effort condition.
Perri et al., 2019	HC N=29 (8F) Mean age 36 (SD 13)	Go-No Go variation		Insular pN1 amplitude not modulated by stimulus complexity, rather related to salience and awareness of perceptual aspects. Insula pP1 amplitude large for complex stimulus , reflecting perceptual association with motor demands (or sensory-motor awareness). Insular pP2 amplitude larger for complex and target stimuli than simple and non-target.
Wang et al. 2017* EEG ROIs (parietal and frontal electrode sites)	HC N=18 (7F) Mean age 22.06 (SD 1.66)	Cognitive Mental Math Task	Reward/Feedback anticipation: Reward/Feedback receipt:	↑ SPN during high effort condition vs. low effort = ↑ anticipatory attention to upcoming performance feedback. P300 in high effort condition vs. low effort = ↑ motivational significance assigned to outcomes of high effort tasks. Significant main effect of caudality of electrodes: P300 least positive in the central area. FRN more positive in the high effort condition and in the frontal area. Successes elicited less negative FRN in high effort conditions vs. low effort.
Yi et al. 2020* EEG	HC N=32 (16F) Mean age 21.25 (SD 1.59)	Effort-Reward Task (adaptation of a cognitive mental math task)	Reward Anticipation:	↑ SPN when high potential rewards were anticipated vs. low potential rewards, particularly after low effort tasks. - SPN larger over right hemisphere vs. left. No SPN difference between high reward and low reward after high effort expenditure.

Table 2 (continued)

Authors & Imaging Methodology	Group & Demographics	Task	Variable of Interest	Neuroimaging Results
Zhang & Zheng 2022* EEG	HC N=32 (17F) Mean age 22 (SD 3.16)	Modified Monetary Incentive Delay Task	Reward Receipt: Effort Anticipation:	RewP and P3 more positive for high rewards vs. low rewards in frontal and parietal areas. High effort generated greater ERP amplitudes than low effort. ↑ CNV for low-effort vs. high-effort condition. SPN more negative for high-effort vs. low-effort condition. ↑ CNV for the gain relative to neutral condition. SPN more negative for gain condition vs. neutral over the right hemisphere. No significant incentive and effort interactions during anticipation. P3 amplitude difference between gain vs. neutral trials during effort expenditure were > during high-effort vs. low-effort tasks. ↑ P3 amplitudes for high-effort condition vs. low-effort. ↑ P3 for gain condition vs. neutral.
Electrode sites (Fp1, Fp2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz, O2)			Reward Anticipation: Reward-Effort Integration: Effort Expenditure:	

WB = whole brain; ROI = region of interest; fMRI = functional magnetic resonance imaging; EEG = electroencephalogram; HC = healthy controls; ADHD = attention deficit hyperactivity disorder; SCZ = schizophrenia; F = female; SD = standard deviation; PFC = prefrontal cortex; vmPFC = ventromedial prefrontal cortex; dlPFC = dorsolateral prefrontal cortex; dmPFC = dorsomedial prefrontal cortex; MFG = medial frontal gyrus; OFC = orbitofrontal cortex; VS = ventral striatum; ACC = anterior cingulate cortex; dACC = dorsal anterior cingulate cortex; NAcc = nucleus accumbens; al = anterior insula; SN = substantia nigra; SMA = supplementary motor areas; M1 = primary motor cortex; RCZ = rostral cingulate zones; PCC = posterior cingulate cortex; PPC = posterior parietal cortex; IPS = intraparietal sulcus; FP = frontal pole; FG = Fusiform Gyrus; FEF = frontal eye field; IPL = inferior parietal lobe; SPL = superior parietal lobe; IPC = inferior parietal cortex; ITG = inferior temporal gyrus; MTG = middle temporal gyrus; LG = Lingual Gyrus; R = right; L = left, BOLD = blood-oxygen-level-dependent imaging; SV = subjective value; SPN = stimulus-preceding negativity; FRN = feedback-related negativity; CNV = contingent negative variation

* neuropsychological task does not include an element of choice

Choice probability

Of the EEfRT fMRI studies, one found significant nucleus accumbens, and cingulate cortex signals related to choice probability Huang et al., 2016 (see Fig. 2e). Of the EEfRT-variation studies, one combined fMRI/DTI study identified increased SMA, M1, and cingulate motor area activation related to choice probability Bonnelle et al., 2015, and one combined fMRI/sMRI study identified decreased right caudate activity related to hard tasks with high probability Yang et al., 2016.

Patterns of neural activation associated with other identified effort-based decision-making constructs

Reward valuation

One fMRI EEfRT study reported recruitment of the vmPFC, and dACC Arulpragasam et al., 2018. Another fMRI study using an alternative EEfRT task identified the VS and vmPFC as coding the subjective value of delayed rewards with decreasing activity with longer delays Prévost et al., 2010.

Effort anticipation/effort prospect

Of the EEfRT fMRI studies, one study demonstrated recruitment of pre-SMA regions Klein-Flugge et al., 2016, one study found VS activity related to anticipation and initiation of effortful movement Suzuki et al., 2021, and one study found no brain regions encoding effort cost Arulpragasam et al., 2018. Of the EEfRT-variation studies, one study identified increased left primary sensory cortex activation Aridan et al., 2019, one study identified increased dACC and decreased vmPFC activity related to expected costs of the chosen option Nagase et al., 2018, one study identified decreased dACC activation related to increased effort expectation Croxson et al., 2009 and one study found increased SMA, M1 and cingulate motor activity related to the anticipation of an effortful motor response Bonnelle et al., 2015. One study using an alternative EBDM task found greater dACC, pre-SMA and VS activation related to effort anticipation Kurniawan et al., 2013. An additional alternative EBDM fMRI study identified superior parietal lobe, frontal eye field, fusiform gyrus, lingual gyrus, dmPFC and dlPFC, SMA and occipital pole activity related to the anticipation of hard tasks relative to easy ones Stoppel et al., 2011. One EBDM EEG study identified larger contingent negative variation (CNV) amplitudes for low- versus high-effort conditions, and more negative stimulus-preceding negativity (SPN) amplitudes for high- versus low-effort conditions Zhang & Zheng, 2022.

Reward anticipation

Of the EEfRT fMRI studies, one study identified greater vmPFC activity when reward information was presented first Arulpragasam et al., 2018. One EEfRT EEG study found no significant signals when waiting for reward after easy and hard tasks Giustiniani et al., 2020. Of the EEfRT-variation fMRI studies, one study identified increased dACC and insula activation Croxson et al., 2009 and one study found increased SMA and cingulate motor area activation related to reward expectancy Bonnelle et al., 2015. One alternative EBDM fMRI study identified superior parietal lobe, medial temporal gyrus, medial PFC and occipital pole activity in anticipation of high vs. low rewards Stoppel et al., 2011. One alternative EBDM EEG study found greater SPN amplitudes during high effort conditions relative to low effort conditions suggesting that individuals devoted greater anticipatory attention to upcoming performance feedback when they exerted more effort Wang et al., 2017. There were no significant effects of caudality or laterality of EEG electrode placement Wang et al., 2017. A second alternative EBDM EEG found larger SPN amplitudes over right hemisphere when high potential rewards were anticipated vs. low potential rewards, particularly following a low effort task Yi et al., 2020, while a third EEG study identified increased negative-going SPN amplitudes only for low-effort versus high-effort trials Bowyer et al., 2021. A fourth EEG study identified larger CNV and more negative SPN amplitudes for gain relative to neutral conditions, particularly over the right hemisphere Zhang & Zheng, 2022.

Effort expenditure

Of the EEfRT fMRI studies, one study identified increased SMA and putamen activation Klein-Flugge et al., 2016, one showed increased dorsal VS activity related to initiation of effortful movement Suzuki et al., 2021, and one study identified increased Nacc activation related to increased willingness to expend high-level effort Huang et al., 2016. One EEfRT sMRI study found no association between NAcc volume and subjects' willingness to exert effort Mathar et al., 2016. Of the EEfRT-variation fMRI studies, one identified vmPFC activity related to decreasing physical-demand Aridan et al., 2019, one found greater posterior parietal/occipital cortex, and middle- and posterior cingulate cortex, left postcentral gyrus, and left precuneus activity during hard task Culbreth et al., 2020, and one study identified increased NAcc and cingulate cortex activity related to No-risk/No-effort choices versus No-risk Maximum-effort Bernacer et al., 2019b. One EEfRT-variation EEG study identified increased M1 and cingulate cortex amplitude related to effort costs Harris & Lim, 2016. One alternative EBDM fMRI study found

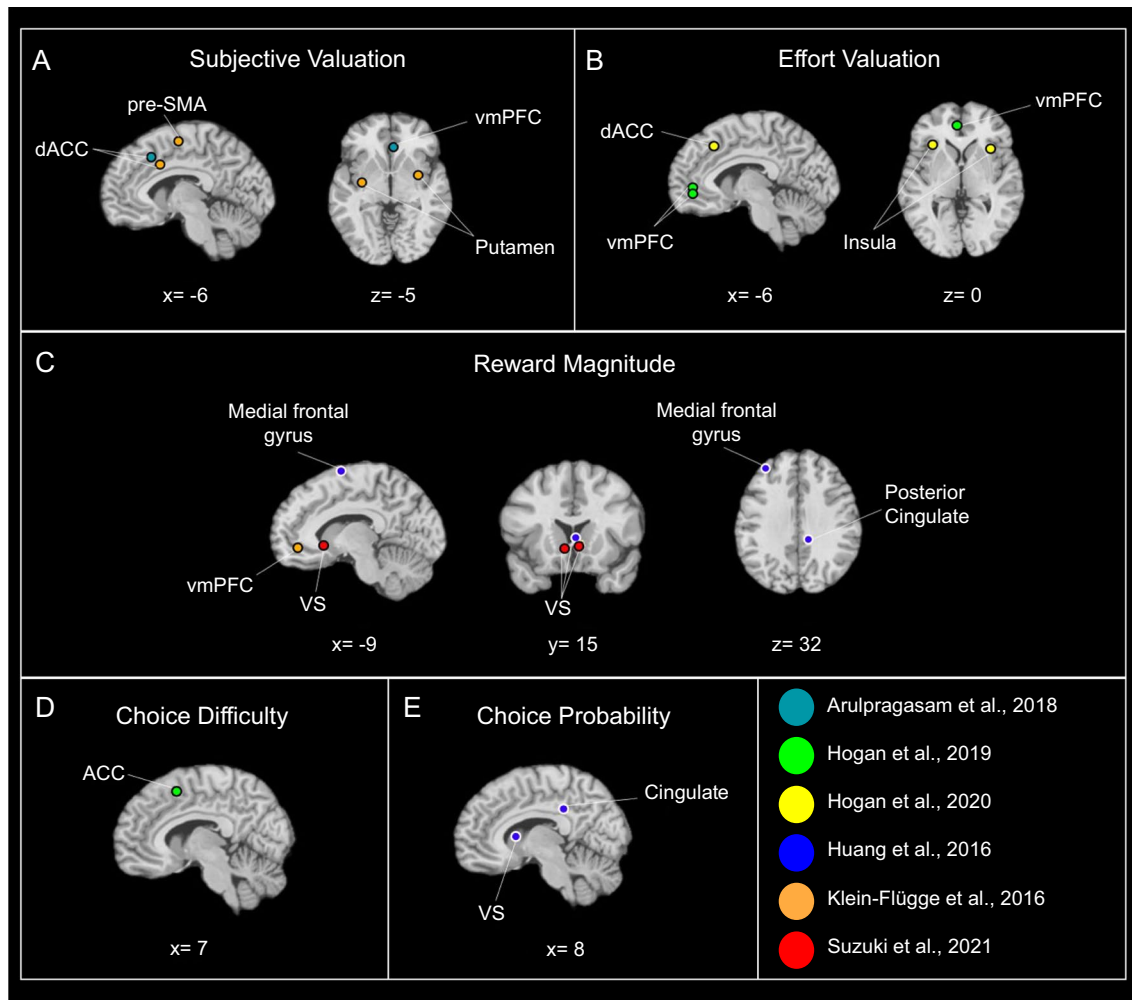


Fig. 2 Brain regions associated with effort-based decision-making constructs observed in studies using the Effort-Expenditure for Rewards Task. A) Subjective valuation recruits the dorsal anterior cingulate cortex (dACC) Arulpragasam et al., 2018; Klein-Flügge et al., 2016 pre-supplementary motor areas (pre-SMA) Klein-Flügge et al., 2016 the ventromedial prefrontal cortex (vmPFC) Arulpragasam et al., 2018 and bilateral putamen Klein-Flügge et al., 2016. B) Effort valuation recruits the vmPFC Hogan et al., 2019, dACC, and

bilateral insula Hogan et al., 2020. C) Reward magnitude recruits the vmPFC Klein-Flügge et al., 2016, medial frontal gyrus Huang et al., 2016, bilateral ventral striatum (VS) Suzuki et al., 2021 and posterior cingulate Huang et al., 2016. D) Choice difficulty recruits the dACC Hogan et al., 2019 and E) Choice probability recruits the VS and cingulate Huang et al., 2016. A 5-mm sphere was placed around reported coordinates from each study

decreased vmPFC and VS activation related to increased effort Westbrook et al., 2019. One alternative EBDM fMRI study identified increased ACC, superior parietal lobe, aI, posterior OFC, frontal eye field, inferior parietal cortex, midbrain/substantia nigra and striatum activity for hard versus easy tasks Stoppel et al., 2011. One alternative EBDM EEG study found greater parietal (Cz, CPz and Pz) amplitudes during high-effort relative to low-effort tasks Ma et al., 2014. A second alternative EBDM EEG study identified more positive Reward Positivity (RewP) ERP in high-cognitive effort versus low-cognitive effort trials Bogdanov et al., 2022, while a third EEG study identified increased effort-P3 amplitudes following high-effort

expenditure vs. low-effort expenditure trials, no significant effects of effort level on RewP amplitudes, and increased feedback-P3 amplitude following low-effort vs. high-effort expenditure Bowyer et al., 2021. A fourth EEG study demonstrated increase P3 amplitudes during effort expenditure for both high-effort and gain conditions relative to low-effort and neutral conditions Zhang & Zheng, 2022.

Prediction error/expectation violation

One EefRT fMRI study demonstrated dACC and insula activity encoding prediction error signaling Arulpragasam et al., 2018 and one EefRT-variation fMRI study identified

increased dACC and pre-SMA activation related to behavioural inconsistency Bernacer et al., 2019b.

Reward-effort integration

Of the EEfRT fMRI studies, one study identified SMA and dACC integrating information from reward and effort cues during the decision phase Klein-Flugge et al., 2016 and one study identified the putamen integrating effort and reward information Arulpragasam et al., 2018. One study demonstrated VS sensitivity to discounted reward values by effort, where VS response to reward was significantly lower after effort cues Suzuki et al., 2021. Of the EEfRT-variation fMRI studies, one study demonstrated decreased vmPFC activation, and increased dACC and pre-SMA activation related to cost–benefit weighing Bonnelle et al., 2015. One alternative EBDM fMRI study found increased M1 activity associated with the subjective value of high reward/high effort choices Prévost et al., 2010. One alternative EBDM fMRI study identified one single activation cluster within the left primary visual cortex during the integration of anticipatory reward- and effort-related cues Stoppel et al., 2011. Increased superior parietal lobe, striatum, midbrain/substantia nigra and frontal eye field activation is also observed during the integration of reward- and effort-related targets Stoppel et al., 2011. One alternative EBDM EEG study found more negative feedback-related negativity (FRN) signals during neutral feedback relative to positive feedback and more positive P300 amplitudes during positive feedback relative to neutral feedback in the high effort condition. No significant differences emerged during low effort trials Ma et al., 2014. A second alternative EBDM EEG study demonstrated trending RewP amplitude differences between gains and losses during low-effort vs. high-effort condition, and trending feedback-P3 amplitude difference between high- and low-effort conditions for gains vs losses Bowyer et al., 2021. Lastly, a third alternative EBDM EEG study found no significant incentive and effort interactions during anticipation phases of a modified Monetary Incentive Delay Task, but larger P3 amplitude difference between gain versus neutral trials during high-effort relative to low-effort tasks Zhang & Zheng, 2022.

Discussion

This review systemically synthesized studies examining neural components of costs/benefit analysis to shed light on the neurobiology guiding EBDM. Findings across 20 studies illustrate cognitive valuation systems, highlighting roles for the vmPFC, dACC, pre-SMA, M1, ACC, PCC, insula and VS in EBDM across healthy and psychiatric populations.

Understanding how subjective value is represented in the brain, and how effort costs are represented and integrated, is critical for value-based decision-making. When evaluating reward and effort cues, and monitoring chosen and unchosen options, EBDM paradigms identified a network including the vmPFC, dACC, insula, SMA, motor cortices, PPC, PCC and VS in healthy individuals Arulpragasam et al., 2018; Bernacer et al., 2019b; Croxson et al., 2009; Harris & Lim, 2016; Klein-Flugge et al., 2016; Prévost et al., 2010; Westbrook et al., 2019. ROI investigations implicated specific brain regions in subjective valuation Bernacer et al., 2019b; Croxson et al., 2009; Harris & Lim, 2016; Prévost et al., 2010; Westbrook et al., 2019 which were further substantiated by whole-brain analysis Arulpragasam et al., 2018; Klein-Flugge et al., 2016; Prévost et al., 2010; Westbrook et al., 2019. EEfRT paradigms can emphasize the dynamics of choice by independently varying effort and reward levels, thereby tracking the neural substrates of expectations and their violation. A computational modeling approach showed differential recruitment between subjective aspects of expectation and discounting Arulpragasam et al., 2018; specifically, vmPFC recruitment occurred for expected subjective values, when reward information was presented first, highlighting its role in forming reward-based predictions Arulpragasam et al., 2018; Rushworth et al., 2012. Accordingly, another EEfRT variation study also demonstrated how greater vmPFC amplitude related to net values (subjective value – effort cost) further underscoring its role in reward processing Harris & Lim, 2016. Although vmPFC activity relates largely to aspects of expectation Rushworth et al., 2012, reward/effort signals also modulate activity throughout distinct striatal regions Croxson et al., 2009. Localization of function across striatal regions is also reported with cost–benefit cue-related activations on an EEfRT variation task and supports an integrative role in the VS, but more of a segregation of information across other adjacent areas. For example, a delay and effort discounting task demonstrated how increased VS activity encodes the subjective value of delayed rewards Prévost et al., 2010, suggesting a central role monitoring current versus long-term reward values. Additionally, greater VS and midbrain activation differentially relate to high benefit values, specifically to high rewards discounted by effort Croxson et al., 2009. Consistent with the VS signaling expected subjective values driven by reward size Diekhof et al., 2012, increases in expected reward magnitude were strongly related to rostral VS activity Croxson et al., 2009. In contrast to the rostral VS, the putamen showed increased signaling as anticipated effort expenditure decreased Croxson et al., 2009. Thus, there is some evidence for the VS integrating cost–benefit information to form a net valuation signal, whereas the putamen may provide a segregated signal about costs or benefits in isolation Croxson et al., 2009.

Reciprocally, with decreasing subjective value, the dACC and anterior insula increase activity, highlighting an important role in encoding subjective value discounting, as expectations are updated, or violated Arulpragasam et al., 2018; Prévost et al., 2010. This demonstrates critical differences in how the brain computes and monitors value-based predictions during effortful choices Arulpragasam et al., 2018; Rushworth et al., 2012. The dACC, insula, SMA and putamen also play key roles in encoding the subjective value between chosen and unchosen options; these regions are particularly active when individuals alternate between choices, but show decreased activity when decisions remain consistent Bernacer et al., 2019b; Klein-Flugge et al., 2016. More specifically, the dACC signals a subjective value difference: increasing activity during unchosen options, while decreasing activity during chosen options Klein-Flugge et al., 2016; Rushworth et al., 2012. Likewise, EEfRT-variation studies show increased dACC activation relating to subjective value in inconsistent decisions Bernacer et al., 2019b; Rushworth et al., 2012. Behaviorally, subjective valuation also decreases on highly inconsistent/unpredictable response patterns Bernacer et al., 2019b. These results accord with previous studies highlighting the dACC role in choice difficulty and inconsistent decisions Centanni et al., 2021; Rushworth et al., 2012; Shenhav et al., 2014, suggesting that dACC activation in response to difficulty or conflict may be due to evaluating behavioural change and choice monitoring Kolling et al., 2016; Rushworth et al., 2012. Similar to fMRI, increased EEG amplitudes in the dmPFC, precuneus, and PPC relate to valuation processes more generally Harris & Lim, 2016. Together, these findings underscore the dACC role in monitoring choice expectations for reward maximization (i.e., attentional and deliberate goal-directed behaviours while monitoring unchosen options), whereas more dorsal areas of the brain like the PCC are more important for consistent decisions/monitoring chosen options. Alternative EBDM tasks additionally demonstrate increased vmPFC, VS, PCC, and dACC activation relative to subjective valuation more generally Westbrook et al., 2019, suggesting a shared network integrating information from multiple sources.

Effort valuation

Regions encoding effort costs, when separated from rewards, recruit vmPFC Hogan et al., 2019, dACC Hogan et al., 2020; Prévost et al., 2010, insula Hogan et al., 2020; Prévost et al., 2010, basal ganglia and ventrolateral prefrontal cortex Bonnelle et al., 2015. The vmPFC activity increases relative to subjective value of future efforts, suggesting this region encodes subjective costs underlying prospective physical effort choices Hogan et al., 2019. The dACC and bilateral insula also increase activation in relation to chosen effort

value Hogan et al., 2020; Prévost et al., 2010, suggesting a role for both the ACC and insula in cognitive control required at the time of choice Centanni et al., 2021; Hogan et al., 2019. These regions may represent a sustained control network processing multiple demands, and maintaining the overall reward value of an environment to prevent behavioural errors Centanni et al., 2021; Rushworth et al., 2012. Indeed, recruitment of the medial PFC and ACC during both effort valuation and effort expenditure in preclinical models, support these findings Rudebeck et al., 2006; Rushworth et al., 2012; Walton et al., 2009. Nevertheless, not all studies show dACC activity when effort costs are presented alone Arulpragasam et al., 2018, suggesting a role in expectation formation/strategy updating rather than effort valuation processes. Decreased cingulate motor and basal ganglia areas relate to effort valuation in healthy participants, suggesting that cingulate areas of the brain play a crucial role in signaling action requiring substantial effort Bonnelle et al., 2015. Increased cortical thickness in the hand knob region of the precentral gyrus is linked to higher subjective effort costs Umesh et al., 2020, suggesting that brain characteristics beyond functional activity may influence effort valuation processes Galaro et al., 2019. Therefore, isolating effort valuation from reward information gives rise to a network of brain regions including frontal and motor cortices which reflect participants' preparedness for completing future effortful tasks.

Reward magnitude

Recruitment of vmPFC and VS areas corresponding with reward magnitude Giustiniani et al., 2020; Klein-Flugge et al., 2016; Suzuki et al., 2021; Westbrook et al., 2019 are consistent with a parametric relationship and existing evidence of activation in these areas linked with increasing reward magnitudes more broadly Croxson et al., 2009; Kroemer et al., 2014; Peters & Büchel, 2010; Schmidt et al., 2012; Skvortsova et al., 2014. The vmPFC increases activation to reward-seeking behaviors Klein-Flugge et al., 2016, further supporting its role in forming reward-based predictions Rushworth et al., 2012. While central during anticipatory phases of decision-making, the vmPFC also plays a unique role during reward consumption; MIDT studies show how vmPFC activity during reward outcomes correlates with the subjective value of the reward received Oldham et al., 2018. Further, an EEfRT variation task applying EEG showed vmPFC activity increases following reward consumption; in the context of delayed updating of reward value, a focused signaling on immediate outcomes could maintain maladaptive decision-making strategies Giustiniani et al., 2020.

Although the VS is implicated in *expected subjective values* Arulpragasam et al., 2018, its function in effort-based

decision-making can be specified to reward-related information Suzuki et al., 2021. Reward anticipation beyond EBDM recruits the VS, highlighting its role in forming initial prediction signals Galtress et al., 2012; Haber & Knutson, 2010; O'Doherty et al., 2004. Additionally, the VS is sensitive to temporal properties of anticipation (i.e., discounting), as activity increases with preference for immediate rewards Cooper et al., 2013; Hariri et al., 2006, suggesting its role in receiving rewards and forming positive reward expectations signals Oldham et al., 2018. Indeed, delays of only a few seconds on delay discounting paradigms decrease signaling of predicted reward values in the VS, indicating a temporal sensitivity to reward responses Gregorior-Pippas et al., 2009. Beyond EBDM paradigms, studies using the MIDT in healthy participants demonstrate distinct anticipation and outcome processes with reward anticipation linked to VS activation, and reward receipt linked to vmPFC activation Breiter et al., 2001; Knutson et al., 2000, 2001, 2003; McClure et al., 2004. Similarly, VS and vmPFC activation relate to greater rewards on EEfRT variation tasks Westbrook et al., 2019, suggesting a joint valuation network; significant increases in activation with increasing reward magnitudes and significant decreases in activation with increasing efforts Westbrook et al., 2019.

Choice difficulty

Studies separating choice difficulty from effort valuation show that ACC activity may result from cognitive control associated with choice difficulty regarding decisions about effort, rather than effort valuation per se Hogan et al., 2019. A frontoparietal network, including dACC, dlPFC and IPS activation during difficult trials on a Cognitive Effort Discounting Task, highlights greater sensitivity to decision difficulty than subjective valuation Westbrook et al., 2019. Furthermore, 'cost-benefit' weighing – which becomes more difficult to evaluate when costs and benefits are of similar magnitudes – negatively correlated with vmPFC BOLD responses, and positively correlated with dACC and pre-SMA activity Bonnelle et al., 2015, suggesting that vmPFC activity may also be sensitive to aspects of decision ease/difficulty Bonnelle et al., 2015. Further, positive correlations with dACC and pre-SMA activity may suggest more brain resources needed to prepare for and perform effortful tasks, and thus, higher subjective experiences of effort costs Bonnelle et al., 2015. Consistent with previous EBDM studies, these studies highlight the dACC role in processing choice difficulty Hogan et al., 2019 and underscore SMA activation in preparation for more difficult motor tasks Kurniawan et al., 2013. Activation in the middle cingulate cortex and PCC also show increased BOLD signals during difficult decisions Culbreth et al., 2020 further supporting the role of cingulate areas in decision-making difficulty. Nonetheless,

not all studies show dACC activity correspondence with effort magnitude Arulpragasam et al., 2018; Chong et al., 2017. Individuals might avoid more difficult tasks because error rate is higher, not because of effort costs, and as such, the distinction of this area's activity between physical exertion or more generalized decision-making processes needs clarification.

Activity in the SMA Bonnelle et al., 2015, cingulate areas Bonnelle et al., 2015; Huang et al., 2016, M1 Bonnelle et al., 2015 and caudate Huang et al., 2016; Yang et al., 2016 also correlate with choice probability, particularly in anticipation of effortful motor responses Bonnelle et al., 2015. These regions may play a critical role in monitoring physical exertion; the higher the probability of accepting an offer, the greater the motor preparation in anticipation of effort. Indeed, functional connectivity between the ACC and SMA is decreased with behavioural apathy Bonnelle et al., 2015 further characterizing the role of this network in maintaining dysregulated effort allocation. Using the traditional EEfRT task, the right caudate decreases activation when contrasting high and low probabilities in participants with MDD, suggesting that disrupted caudate signaling may underlie motivational anhedonia in MDD Yang et al., 2016. Cortical regions including the temporal and frontal lobes calculate valuation information and subsequently modulate subcortical activation; altered connectivity in MDD may underlie motivational anhedonia and shift choices away from high-cost/high-reward options Kurniawan et al., 2010. Similarly, participants with schizophrenia have less neural response in the NAcc, posterior cingulate gyrus and left medial frontal gyrus on high-probability trials compared to healthy participants on the EEfRT task Huang et al., 2016 suggesting that this network may be involved in reducing willingness to allocate effort. Outside of EBDM, neuroimaging studies of motivational deficits in MDD and schizophrenia highlight dysfunctions of the caudate and NAcc during decision-making processes Kurniawan et al., 2010; Pizzagalli et al., 2009; Salamone et al., 2007a; Treadway et al., 2012, consistent with the idea of a shared network maintaining inability to initiate behavior/physical engagement.

Clinical implications

Identifying key neural processes involved in choice behaviors has important clinical implications. Current pharmacological interventions such as selective serotonin reuptake inhibitors (SSRIs) can negatively impact EBDM processes Presby et al., 2021. For example, preclinical models demonstrate that SSRIs behaviorally suppress high effort activity Presby et al., 2021, exacerbate motivational deficits underlying psychiatric conditions Marin & Wilkosz, 2005 and maintain EBDM impairments Yohn et al., 2016. Animal models have also highlighted the implication of dopamine (DA) in

EBDM; decreasing DA in the NAcc shifts preferences to low-cost/low-reward options while enhancing DA increases high-cost/high-reward choices Bardgett et al., 2009; Salamone et al., 2007b, 2009. These findings are also modeled in human studies, whereby *d*-amphetamine (an indirect DA agonist) enhanced willingness to exert effort when reward probability was lower and did not alter effects of reward magnitude on willingness to exert effort Wardle et al., 2011. Importantly, amphetamine-based drugs additionally increased motivation to invest both the cognitive and physical effort in individuals with attention-deficit/hyperactivity disorder relative to healthy controls, thus providing evidence for catecholamines in motivating effortful behaviours Chong et al., 2023. Neuronal activity in the subthalamic nucleus, the most common target for deep brain stimulation in Parkinson's disease, has also been shown to encode the subjective value of both effort and reward information required for cost–benefit computations Baunez & Lardeux, 2011. Therefore, DA replacement therapy (i.e., levodopa) may strengthen links between subthalamic nucleus activity and behaviours, leading to an increased acceptance for efforts associated with low rewards Zénon et al., 2016.

While neuroimaging studies of EBDM demonstrate decreased activation of specific subcortical regions in schizophrenia Huang et al., 2016, depression Yang et al., 2016, and small vessel cerebrovascular disease Saleh et al., 2021, using novel non-invasive neuromodulation techniques, such as transcranial direct current stimulation (tDCS), can be a promising treatment intervention for upregulating dysfunctional EBDM circuits. For example, stimulating the frontopolar cortex using anodal tDCS can increase the amount of cognitive and physical effort participants were willing to expend Soutschek et al., 2018. Furthermore, tDCS strengthens the function of cost–benefit computations Soutschek & Tobler, 2020, and transcranial alternating current stimulation over dmPFC increases the willingness to exert effort for rewards Soutschek et al., 2022, highlighting changes in goal-oriented behaviors following stimulation. Neurologically and psychologically, healthy participants receiving anodal stimulation of the dlPFC exert more effort on trials with higher reward magnitudes and on trials with lower probability of receiving rewards Ohmann et al., 2018, highlighting the efficacy of stimulating the dlPFC in increasing motivation in instances where rewards/benefits are not guaranteed. Further, one EEfRT fMRI study demonstrated increased activation in posterior parietal/occipital cortex, the middle cingulate cortex, the PCC, left postcentral gyrus and left precuneus during ‘hard task’ choices in both individuals with schizophrenia and healthy controls Culbreth et al., 2020. Therefore, upregulating the activity of prefrontal regions may hold potential as a treatment target to offset increased activation in functionally connected decision-making regions. Nonetheless, downregulating reward-related process

also demonstrates promising effects, as in the case for bipolar disorder Nusslock & Alloy, 2017, depression Ng et al., 2019 and addictions Sazhin et al., 2020 whereby specific aspects of the disorder can manifest with elevated responses to reward. A clearer mechanistic understanding of the functions of neurostimulation could greatly improve motivational deficits in disorders characterized by low motivation.

Beyond neurostimulation, network changes also occur with shifts in environmental and internal states. Habit acquisition stemming from physical fitness programs lead to changes in neural patterns, where the functional connectivity between the striatum, ACC and amygdala are strengthened when making behavioural choices that involve no risk and no effort Bernacer et al., 2019b. Although no significant associations are observed between the structural properties of the NAcc and the willingness of participants with obesity to expend effort for rewards Mathar et al., 2016, shifts in cost processing following habit formation appear to attenuate effort costs in EBDM tasks Bernacer et al., 2019b, suggesting that executive functioning processes like decision-making are not fixed, but rather modifiable and make for a suitable target for treatment. Furthermore, fatigue has important implications for choice behavior. Behaviorally, people are more likely to exert effort in situations when fatigue is low Müller et al., 2021. However, as fatigue increases, high effort/low reward trials that were once deemed worthy of the costs at the beginning of decision-making task lose all value Müller et al., 2021. This suggests that changes in the willingness to work can also be a reactive process, resulting from changes in internal states rather than shifts in valuation and expectation Müller et al., 2021 and is particularly relevant when considering the clinical utility of EBDM paradigms with clinical disorders affected by fatigue Chaudhuri & Behan, 2004; Wolpe et al., 2024. At a neural level, the integration of effort valuation and levels of fatigue recruits the VS and frontal pole Müller et al., 2021. Moreover, evidence suggests that the medial frontal gyrus processes longer-term unrecoverable states of fatigue, impacting both EBDM, performance, and choice behavior in other decision-making tasks more broadly, while the anterior rostral cingulate plays a key role in sustaining motivation during effortful task Müller et al., 2021. As such, different brain regions are involved in signaling different facets of fatigue (chronic vs state) Müller et al., 2021. Understanding natural shifts in connectivity resulting from environmental and internal states has large clinical implications and may be a suitable target for treatment interventions.

Strengths, limitations and future directions

With the exception of a meta-analysis Lopez-Gamundi et al., 2021, this is the first study to systematically review the literature examining the structural and functional

anatomy across specific EBDM constructs and psychiatric populations. Limitations include the predominant use of monetary rewards (with the exception of one study using erotic images Prévost et al., 2010 across paradigms; while essential for establishing/validating reward processing trends, future studies should examine how effort-, reward- and valuation-related process differ across incentive types (e.g., food, substances and behaviors). Importantly, EEG studies may also be limited in their capacity to identify activation in particular subcortical regions. Additionally, effort modalities across studies are diverse (e.g. physical/cognitive/financial effort), limiting findings and conclusions. Inconsistencies in choice variability (i.e., increased selection of high-effort tasks versus disengagement), valuation differences (i.e., social economic status impacts on valuation of monetary reward), state and trait effect may also all contribute to performance differences between psychiatric disorders. Additionally, not all studies included in our systematic review used an effort-based decision-making task that incorporate choice elements Croxson et al., 2009; Kurniawan et al., 2013; Ma et al., 2014; Stoppel et al., 2011; Vorobyev et al., 2015; Wang et al., 2017; Yi et al., 2020; Zhang & Zheng, 2022. Some studies also introduce model-derived estimates that model subjective or effort valuation [e.g. Arulpragasam et al. 2018, Klein-Flugge et al. 2016, Hogan et al. 2020]; explicitly fitting these parameters at the participant level can minimize or eliminate within-individual differences and maximize detection of the experimental effort values of interest. These model-derived values can further, through paradigm design, build functions to model shifting subjectivity parameters with specific experimental manipulations. This can work to parse out potential overlap between effort valuation signals that may be incorporated into the subjective valuation regressors and instead focus on group- or population-level characteristics, rather than individual-level differences. In this way, integrating computational modeling with neural analysis can provide a neurobiological account of neural comparator processes as effort values change. How well individuals understand task instructions may also influence performance. Large-scale replication studies as well as studies comparing across psychiatric conditions are therefore needed to generate valid conclusion. This work is important in establishing EBDM constructs and identifying noticeable characteristics in healthy populations, which can subsequently inform findings across psychiatric conditions. Nevertheless, meta-analyses on the topic are warranted to identify neural regions that may not be captured by traditional methods and may be implicated in EBDM, thereby reducing potential reinforcing biases in the literature, especially considering that qualitative reviews tend to focus less on lack of effects. Given that we observed no effects related

to effort valuation, reward magnitude and choice difficulty, these constructs merit further investigation. In our review, differences in EBDM tasks, sample characteristics, measured constructs and ROIs, restrict direct comparisons across studies. While our review includes peer-reviewed articles from many countries including the United States Arulpragasam et al., 2018; Culbreth et al., 2020; Harris & Lim, 2016; Hogan et al., 2019, 2020; McGuire & Botvinick, 2010; Prettyman et al., 2021; Suzuki et al., 2021; Umesh et al., 2020, United Kingdom Bonnelle et al., 2015; Croxson et al., 2009; Klein-Flugge et al., 2016; Kurniawan et al., 2010, 2013; Müller et al., 2021; Saleh et al., 2021, China Huang et al., 2016; Yang et al., 2016, Germany Mathar et al., 2016; Soutschek & Tobler, 2020, France Giustiniani et al., 2020; Prévost et al., 2010, Israel Aridan et al., 2019, Spain Bernacer et al., 2019b, Japan Nagase et al., 2018, Switzerland Abivardi et al., 2020, the Netherlands Mies et al., 2018; Westbrook et al., 2019, Belgium Schoupe et al., 2014, Finland Vorobyev et al., 2015, Italy Perri et al., 2019, our inclusion of only English-published work may result in findings from non-English studies being overlooked.

Concluding remarks

EBDM paradigms can disentangle motivational facets on choice behavior. Although heterogeneous regions are recruited, brain networks most implicated include the vmPFC, dACC, SMA, M1, specific cingulate, insular and VS areas. The vmPFC and VS both appear as part of a core valuation network tracking both effort and subjective value and reward magnitude, while the dACC conversely highlights effort costs. The review demonstrates specific brain regions involved in valuation, preparedness and monitoring processes; the vmPFC in forming reward-based predictions, the VS encoding expected subjective values driven by reward size, the dACC in monitoring choice expectations for reward maximization, while SMA, M1 and cingulate motor areas in preparedness to expend effort. A better understanding of these networks and their changing connectivity will provide greater insights into the development, maintenance and treatment of psychiatric conditions characterized by maladaptive EBDM strategies.

Authors' contributions S.B. was responsible for abstract reviews, and interpretation, and drafting, revising and preparing the current manuscript for submission. H.L. contributed to abstract reviews from study inception. J.S. contributed to creating figures and reviews. J.M. contributed to the framework of the project. I.M.B. conceived the idea and scope of reviews contained in the current manuscript. All

authors provided critical feedback and shaped the research, reviews and interpretation of the findings, and approved the final manuscript.

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Data availability All data and materials generated or used during the study are available from the corresponding author by request.

Declarations

Ethical approval Not applicable.

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