The neuroeconomics of work: Computational and neural mechanisms of the dynamics of effort-based decisions

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1.0 Introduction

The motivation to exert effort is fundamental for health, wealth and survival. Reduced motivation is linked to unemployment, poor educational outcomes, and poorer physical and mental health [1–6]. To understand the extensive impact of motivation, research across psychology, economics, psychiatry, neurology and neuroscience is increasingly deploying neuroeconomics inspired paradigms, to understand how we choose whether to exert effort or not [7–12]. This has led to multiple insights into the computational and neural mechanisms underlying effort, its variation between healthy people, and how and why it can be impaired.

Here we outline the most recent work in this field which highlights that there are multiple domains to motivation, various contexts which modulate our willingness to exert effort, and that choosing to exert effort or not dynamically waxes and wanes from moment-to-moment. We review and synthesise this work to move towards a neuroeconomic framework for motivation.

1.1 Effort-based decisions

The concept of effort-based decisions was first considered theoretically in a powerful proposal by Clark Hull[13]. He stated that if animals have a choice between two equally valuable rewards, such as two identical foods of equal size, their behaviour conforms to a 'law of less effort', almost ubiquitously choosing the option that is less difficult to obtain. This effort is not about the probability of succeeding at a task; even when there is no risk that an action will not lead to a reward, more difficult actions are avoided. Effort is therefore a subjective – or at least intrinsic – cost that an animal must pay in order to receive some rewards [9,10,14,15]. More effortful actions discount the value of rewards to a greater degree, such that more difficult tasks will only be pursued over easier ones when that higher exertion can bring a larger reward. In short, we are less likely to pursue food or money if it takes more effort to obtain them.

This theory has given rise to multiple experimental paradigms testing its tenets (**Figure.1.A**). Most tasks take a similar form: participants have to make a series of choices between a more difficult version of a task, such as higher grip force [4,11], more complex arithmetic [16–18], or more switches between cognitive tasks [19–22] that require more effort but will gain more reward, or an easier version of the same task that requires less effort for less reward [23]. While choices vary considerably between people, the vast majority will consistently avoid high effort, only choosing it if the rewards for doing so are larger (**Figure.1.B**). Although decision-making is often used to probe motivation's effects on actions, it is clear that motivation plays a role in multiple phases of behaviour, from how we generate options, decide what to engage in, energise and exert the required control of behaviours, and how we learn from their consequences (**Figure.2**) [3,14,24–26]. Thus, across many phases during a task, our behaviours are only 'worth it' if the effort costs are low and rewards are high.

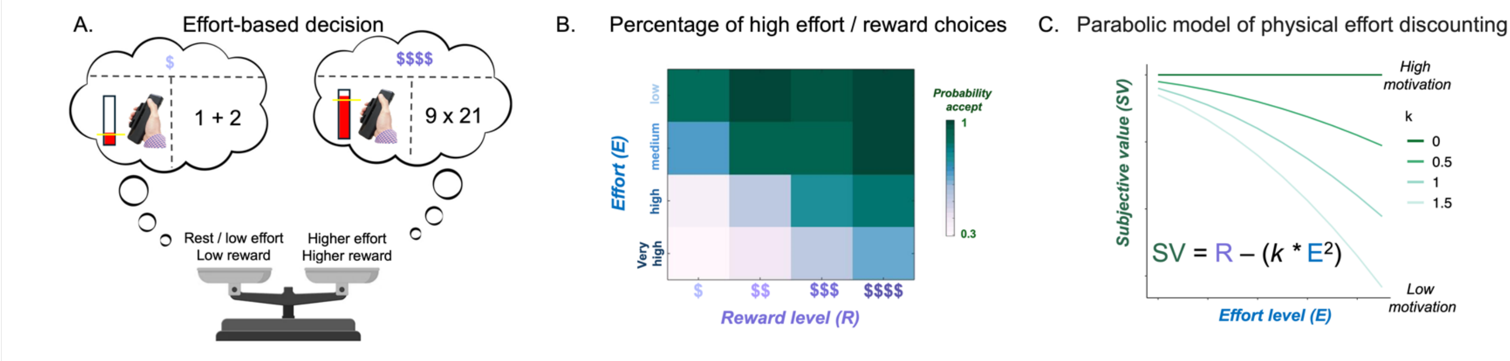

Figure 1. Effort-based decisions and computational models of choices. *A. A typical effort-based decision-making task setup: Participants have to choose between a more difficult version of a task, e.g., higher physical effort (grip force) or a higher cognitive demand (harder maths puzzle), to gain more money, or an easier version of a task that requires less effort for less money. B. Behavioural data from 31 healthy young adults performing a physical effort (grip force) task in which one option was to rest and gain a low reward, and the higher effort option varied in both the effort level and the reward level across trials. When the higher effort and reward option was to exert effort at the easiest level (1) and the reward at stake was high (4, top right), almost all participants consistently chose for the high option. In contrast, when the required effort was high (4) and the reward low (1, bottom left), participants often preferred to rest and gain a low reward. C. An example of how a computational model of effort-based choice works. Choices depend on subjective value – the rewards being devalued or discounted by the costs of the effort. The model assumes that rewards (R) increase subjective value (SV), effort (E) decreases SV, and people discount the rewards by effort idiosyncratically—modelled with a discounting parameter (k). This schematic representation shows variable k changes how someone discounts one level of reward by different levels of effort, with higher values reflecting greater devaluation of rewards. Note that the function and corresponding figure are based on studies that provided evidence for a parabolic model of physical effort discounting.*

1.2 Computational models of effort-based choice

Using algorithms – computational models – to explain how people make decisions is a powerful neuroeconomic approach that can uncover underlying, but hidden, cognitive or neural mechanisms [27,28]. Models can precisely quantify variability between people, and when combined with brain imaging or neurophysiology, can provide a richer understanding of neural mechanisms. Computational models of 'effort-discounting' (**Figure.1.C**) have provided such benefits for understanding effort-based decisions [11,12,29]. Most models assume that choices depend on a computation of subjective value (*SV*), where the level of difficulty of a task - the cost of effort (*E*) - is deducted from the magnitude and value of reward (*R*) on offer [22,30,31]. Thus, subjective value is higher as reward increases or as effort decreases. Variability between people is accounted for through a discounting parameter (typically labelled *'k'*) which is estimated across all the decisions made in the task, summarising the degree to which on average a person discounts reward by effort. A higher *k* reflects a person who devalues reward by effort to a greater degree and thus can be considered less motivated.

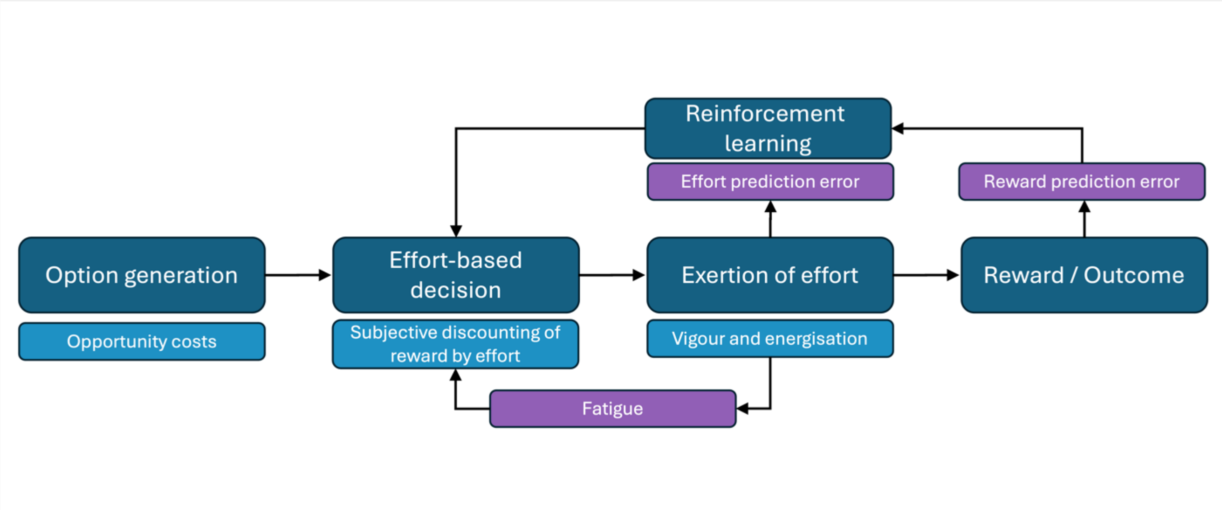

Figure 2. Multiple phases in which motivation effects the allocation of effort. *Motivation can be broken down into different phases. These phases comprise: generating options which is influenced by the opportunity costs of options in the environment; decisions of whether to initiate a behaviour which involves evaluating, ascribing value and choosing; exertion and persistence which involves energising the actions or cognitive control processes to a sufficient degree to succeed; receiving the reward, and learning from one's effortful actions. Throughout each, we must remain motivated in order that we continue to pursue behaviours and cognitive processes with the required vigour and control, meaning that a desire to avoid effort could impact behaviour in multiple ways during tasks. The value of exerting effort is then updated on a moment-to-moment basis, through effort predictions errors, reward prediction errors as well as fatigue. All of these influence the subjective value of exerting effort in a dynamic manner during a task.*

1.3 Brain mechanisms of effort

Studies using this neuroeconomic modelling approach have consistently found a network of anatomically connected fronto-striatal regions of the brain engaged during effort-based choice [4,11,16,22,32–34]. The Blood Oxygenation Level Dependent (BOLD) response in dorsal portions of the anterior cingulate cortex (dACC), ventral tegmental area (VTA), ventral striatum (VS), anterior insula (AI), dorso-lateral prefrontal cortex (dlPFC), and frontal pole (FP) covaries with the subjective value of effort-discounted rewards during fMRI. Converging evidence from studies examining the effects of experimental and acquired lesions to these regions, as well as single-unit recording studies in monkeys, highlights this as a network that is important for deciding whether to exert effort [4]. This network might be involved in motivation across multiple phases of behaviour (**Figure.3**), with the dACC especially also implicated in the top-down control of cognitive processes during task behaviours [24,25,35–39]. Although it is clear that multiple neuromodulators may be involved in effort-based decision-making, most studies have only examined dopamine, finding that boosting dopamine increases people's willingness to choose to exert more effort [8,22,40–43].

Overall, this suggests there is a dopamine driven fronto-striatal circuit (**Figure.3**) that guides decisions, signalling the subjective value of effort-discounted rewards and motivating us to overcome the costs of effort.

2.0 The domains of motivation in different contexts

Motivation is multi-dimensional. We have to be motivated to exert different types of effort for different types of reward in different contexts. In the following sections, we outline the mechanisms underlying effort-based choice in different contexts.

2.1 Cognitive versus physical effort

People find both physically and cognitively demanding tasks effortful and avoid those costs if possible. A consistent finding is that for physical effort, the devaluing effect is nonlinear, with the rewards parabolically discounted as a function of grip strength [22,30,44] **(Figure.1.C)**. This is less clear for cognitive effort, with some studies suggesting rewards are hyperbolically discounted when more difficult peripheral switches of attention are required to obtain them [22]. However this is likely to depend on the nature of the cognitive operations performed [10], with different cognitive processes having a different form to the cost function [45] .

Intriguingly, despite differences in the computational nature of cognitive and physical effort costs, the same regions are implicated in signalling the subjective value of effort-discounted rewards, including the dACC, VS, and AI [22,32] (**Figure.3**). To date, only the dorsolateral amygdala has showed any difference, being engaged during cognitive but not physical effort-based choices [22,46]. Similarly, boosting dopamine has been shown to increase the motivation for both cognitive and physical effort, suggesting significant overlap in the neural mechanisms underlying how we motivate different forms of effort [40,42].

2.2 Prosocial effort: The effort of helping others

Prosocial behaviours – actions that benefit others – have been studied extensively in neuroeconomics [47]. However, the field often overlooked that deciding to be prosocial usually requires us to choose whether to exert effort: for example, deciding whether to help a colleague at work or hold open the door for a stranger [12]. By adapting typical effort-based decisions tasks where one can obtain a reward for self, to include a prosocial condition where people must make a choice and exert effort, but to obtain a reward for a stranger, new insights into prosocial motivation have been revealed. Consistently it has shown that people discount the value of rewards by both cognitive and physical effort to a significantly greater degree during prosocial compared to self-benefitting choices [33,44,48–50]. Moreover, even when people make a choice to help, they exert less energy into high effort actions for others compared to themselves. The degree to which this is the case changes across the lifespan, and varies with psychological traits including empathy and apathy [44,51].

Research has revealed some of the neural mechanisms underlying self-benefitting and prosocial effort-based decisions overlap [33,52] in dACC and AI. However, this is not entirely the case. Damage to portions of the ventromedial prefrontal cortex selectively reduce the willingness to exert effort for others but not ourselves [53]. Moreover, the VTA is engaged only when guiding decisions about whether to exert effort for self, and conversely a separate ACC sub-region, lying in the gyrus (ACCg) is engaged in motivating effort only when it is prosocial [52,54]. Overall, this suggests that while there may be a domain-general system guiding effort-based decisions in multiple contexts, additional systems may be involved depending on the context in which an effort-based choice is made (**Figure.3**).

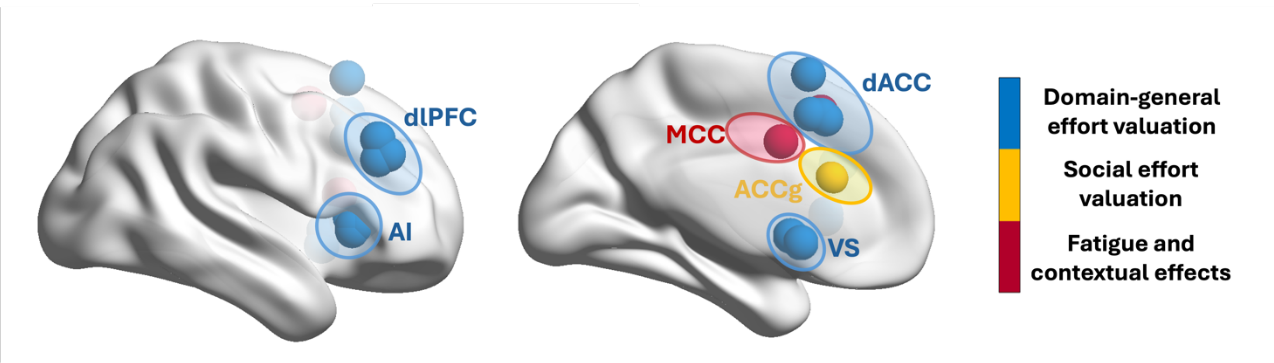

Figure 3. The neural systems guiding effort-based decisions. *Representation of the key regions engaged in deciding whether to exert effort, illustrated using spheres around Montreal Neurological Institute (MNI) standardized peak coordinates from fMRI studies[16,22,32,52,71,129]. Blue are regions in which the subjective value of exerting effort is processed in multiple studies, indicative of a domain-general network involved in deciding whether to exert effort in multiple contexts. Yellow are regions implicated specifically in deciding whether to exert effort to act prosocially and obtain other people rewards. Red are regions involved in processing contextual information, such as fatigue, that shifts the degree to which effort is discounted by rewards, and can switch effort to being valuable. Outline ovals represent approximate location of anatomical regions. Please note the dACC label corresponds to the typically large clusters that extend over cingulate sulcus and pre-SMA that are found in these studies. dlPFC = dorso-lateral Prefrontal Cortex; AI = Anterior Insula; MCC = Midcingulate Cortex; VS = Ventral Striatum; dACC = dorsal Anterior Cingulate Cortex. Visualised with the BrainNet Viewer (https://www.nitrc.org/projects/bnv/). Xia M, Wang J, He Y (2013) BrainNet Viewer: A Network Visualization Tool for Human Brain Connectomics. PLoS ONE 8(7): e68910. doi:10.1371/ journal.pone.0068910*

3.0 The dynamic nature of effort-based choices

The motivation to exert effort is not static, but instead fluctuates from moment-to-moment [55]. Here, we discuss some of the processes underlying these fluctuations, and how computational modelling can capture how they influence effort-based decision-making.

3.1 Learning whether to exert effort

How effortful an action is, and thus which actions to avoid, must often be gradually learned over time. Such 'effort learning' has recently begun to be investigated using tasks inspired by reinforcement learning theory - a hugely influential account for how humans, animals and computers can learn to maximise rewards. Participants have to learn through trial and error how much cognitive or physical effort is required in order to successfully complete a task and obtain rewards (i.e., rather than maximise rewards, they learn to minimise effort costs). People indeed learn to avoid effort and reinforcement learning algorithms, adapted such that higher effort is treated as lower value [34,56–58], can capture this learning process. In these models expectations about the effort required are updated through prediction errors [59,60] computed as the difference between expected effort cost and the actual effort required. These update future expectations about the effort required, allowing us to learn to avoid highly effortful behaviours.

Despite using the same computational rule for learning about effort and reward, and evidence that effort can modulate learning about rewards [61], studies have found dissociations in the brain areas that learn about them. Whilst reward prediction errors are associated with BOLD response in the VS and ventromedial prefrontal cortex (vmPFC), effort prediction errors correlate with activity in right AI and dorsal anterior cingulate cortex extending into pre-supplementary motor area (pre-SMA), the same areas that signal subjective value outlined above **(Figure.3)**. However, during decision-making, expected reward and effort are integrated in an overall value signal in VS [56–58].

3.2 The effects of fatigue on effort-based choice

Decisions of whether to exert effort can be significantly influenced by fatigue. Over time and with increased effort demands, fatigue causes a reduction in both task performance and the willingness to exert future cognitive or physical effort [62–66]. However, these deficits can be alleviated through rest [67].

These findings have been integrated into computational models, explaining how fatigue and rest can dynamically influence the willingness to exert physical effort from moment-to-moment [18,66,68–71]. These models highlight that there are hidden states of fatigue; recoverable and unrecoverable. Both types increase with effort exertion, however, recoverable fatigue decreases with rest, whereas unrecoverable fatigue simply accumulates over time. These fatigue states influence the willingness to exert subsequent effort, by weighting the effort discounting parameter, *k (Section 1.2)*. Higher levels of fatigue increase effort discounting, thus reducing the subjective value of exerting effort.

There is a wide network of brain regions involved in signalling and integrating cognitive and physical fatigue into effort-based decisions. There are two key findings from this research. One is that the VS appears to code subjective value in a dynamic manner, changing its response in line with how much fatigue is increasing the discounting of rewards by effort. However, the components of fatigue are processed in other regions, with the middle frontal gyrus signalling the unrecoverable aspects of fatigue [69–71], whilst the midcingulate cortex (MCC), lying posterior to the dACC, signals recoverable fatigue [71]. This is consistent with the notion that while there is a core network of regions involved in effort-based decisions, the context a choice is made in is signalled in other regions that influence choice behaviour (**Figure.3**).

3.3 The opportunity costs of exerting effort

The time we spend doing one effortful action, is often at the expense of other activities we could be doing [72,73]. This ‘opportunity cost’ imposed by the time doing an action is thought to be determined by the average rate at which you can obtain rewards from your actions in the environment. When average reward rates are high, there is a higher opportunity cost for moving slowly (the 'cost of sloth’), making it worthwhile to exert effort to move faster. Research shows these reward rates influence the ‘vigour’ of effortful movement, in terms of both speed and force production [74–77]. Higher average reward rates also cause people to respond faster and make more errors when exerting cognitive effort [78]. It has also been shown that average *effort* rates influence movement vigour [79] suggesting that both reward and effort influence the opportunity cost of acting in an environment.

How does the brain represent opportunity costs? Animal studies have found that dopamine in the mesolimbic pathway tracks average reward rates [73,80], and indeed pharmacological manipulation of dopamine in humans changes how they make opportunity cost decisions [81,82], as well as influencing movement vigour/force [76,83]. The brain regions involved in tracking opportunity costs also implicate the domain-general circuit we have outlined, including the dACC and AI [84–86].

4.0 Effort-based decisions index motivation impairments in clinical and non-clinical populations

Disruptions to motivation (e.g., apathy, anhedonia and fatigue) are some of the most common symptoms in neurology and psychiatry, but are also present in a less severe form in the healthy population [3]. Effort-based decision tasks, combined with computational modelling, are beginning to offer insight into the underlying mechanisms of these motivational deficits [4,12,23].

4.1 Individual differences in psychological traits are linked to effort-based decision-making

Effort-based decision-making tasks are ideally set up for examining relationships with individual differences in psychological traits, as they can capture variability between participants, and measure this precisely with computational modelling.

Perhaps the most common finding is that the willingness to exert effort is associated with two key traits, apathy (defined as a reduction in goal-directed behaviour) and need for cognition [44,51,87–91]. The willingness to exert cognitive effort has also been associated with self-reported anxiety, cognitive function, behavioural activation, apathy, and self-efficacy [92]. Moreover, the willingness to exert prosocial effort is associated with social dimensions of apathy, whereas effort to benefit oneself is associated with behavioural apathy [44,51]. This suggests that effort sensitivity in different domains of behaviour may be transdiagnostic symptoms that are present in the healthy population.

Studies have shown age-related differences in effort-based decision-making [48,93,94,95,96]. Older adults, compared to younger adults, show increased discounting of rewards by cognitive effort [93,94]. However, the framing of the outcome, either exerting effort to attain a reward or avoid a loss, may influence age-related differences in effort discounting. Both younger and older adults are more willing to exert cognitive effort to avoid a loss than obtain a reward, with no age-related differences[94]. Yet, for physical effort, whilst older adults are again more willing to exert cognitive effort to avoid a loss, younger adults show the opposite pattern, being more willing to exert effort to obtain reward[95]. In young people, an awareness of effort is apparent even in childhood, although it does not appear to carry through into choice behaviour. For example, children are able to identify that higher levels of cognitive task difficulty are more effortful, but show no apparent aversion to choosing higher effort [96]. All of this highlights how variability in the willingness to exert effort is key to understanding motivation in daily life in healthy people.

4.2 Effort and impaired motivation in neurological and psychiatric disorders

Clinical impairments to motivation are typically measured using questionnaires. Whilst useful for measuring symptom severity, these scales rely on patient insight and may not directly map onto cognitive processes. For instance, motivational impairments can be very different if they arise due to a loss of incentivisation by rewards, compared to a heightened sensitivity to the costs of effort. Computational approaches to motivational deficits can be used to discriminate between these, and bridge the gap between clinical assessment and the underlying pathophysiology (e.g., lack of dopamine) [11].

A heightened sensitivity to effort cost has been found in multiple conditions using this approach, including fronto-temporal dementia, Parkinson's Disease (PD), depression, small vessel disease and schizophrenia – all conditions associated with high levels of apathy, anhedonia and fatigue [3,4,97] .

Patients with Parkinson's disease have been repeatedly found to be less willing to invest physical effort for rewards compared to controls. However, when patients are on dopaminergic medication, they choose to invest more effort for rewards relative to off medication [8], an effect that extends to cognitive effort [42]. Similarly, both dopaminergic and serotonergic medications increase the willingness to exert effort in depression [11,98], and dopaminergic deficits are also linked to negative symptoms in schizophrenia [99]. This evidence suggests that impairments to dopamine - alongside other neuromodulators - are a key component of severely impaired motivation and offer a potential avenue for future treatment. Thus, using effort-based decision-making paradigms suggests that augmenting both dopaminergic and serotonergic systems might be key for ameliorating impairments to motivation.

5.0 Future Directions

Since the conception of the law of least effort introduced by Hull, our understanding of the mechanisms of effort-based decisions has progressed. However, there are still many outstanding questions. Here, we offer four possible avenues for future research.

5.1 Neuromodulators

Whilst the dopaminergic cortico-striatal circuit is heavily implicated in effort-based decision-making [100], there is not always a clear functional relationship between dopamine and effort [101]. Work has begun to create a unified account of dopamine that can account for its role in effort processing and its many other putative functions, as well as explaining how dopamine both is and isn't involved in effort processing in different studies [102–104].

As noted above, other neuromodulators beyond dopamine are also likely to be involved in motivating effortful exertion. Serotonin appears to be involved in effort discounting [105–107], encoding effort prediction errors [109], and tracking opportunity costs [110]. There is also evidence implicating other neuromodulators including GABA [111], noradrenaline [112,113], and acetylcholine [114]. One promising avenue may be using magnetic resonance spectroscopy (MRS) in humans to measure metabolites in the brain. For example, accumulation of glutamate could drive fatigue signals [115], and glutamate and other metabolites have been implicated in effort-based decisions [116,117]. Techniques such as MRS, as well as further pharmacological manipulations in humans and animals, will be needed to disentangle the roles of different neuromodulators.

5.2 Oscillatory mechanisms

Above we have highlighted many fMRI studies that provide insight into where in the brain effort is processed. However, there is a growing interest in understanding the temporal dynamics that underlie effort-based decisions, and in particular the neural oscillations that may be a key signature of how the brain processes information. Studies using EEG and MEG have shown that the influence of opportunity costs on cognitive effort has been linked to reduced theta band power [118] and beta band power in medial frontal cortex is also linked to cognitive control allocation and fatigue related time-on-task effects in non-human primates [119,120]. Intracranial EEG (iEEG) and invasive neurophysiological recordings, once only possible in animal models, are now possible in patients, which has opened the possibility of examining neural oscillations in deep structures in humans [121]. This has revealed that beta band power in the basal ganglia tracks moment-to-moment changes in effort in patients with Parkinson's Disease [122]. Advances in neurophysiological methods will likely further transform our understanding of effort processing.

5.3 Ecology

Neuroeconomics research is increasingly inspired by the animal ecology literature. This approach argues that cost-benefit decisions use brain systems that may be conserved across species, thus we can better understand human neuroeconomic decisions by using tasks and theories from ecology [123,124]. One example is the use of 'patch foraging' tasks, where the participant must choose between staying put and foraging for resources in one location ('patch'), or leaving to seek better patches elsewhere. These studies have told us much about reward decision-making during foraging [82,125–127], and many studies are now also examining how effort costs are involved in these decisions [79,128]. Ecological paradigms also allow a wider range of behavioural strategies to be expressed, which can help us understand individual differences [92]. Foraging paradigms therefore offer a means for bringing together the tools of neuroscience, psychology, biology and economics to better understand how we choose to exert effort.

5.4 The effort paradox

Most research in this chapter has treated effort as a cost we try to avoid. However, there is an 'effort paradox', in that sometimes we seek and value effort [129]. This paradox can be seen in many behaviours in everyday life, such as the desire to climb mountains or valuing effort to meet important deadlines. Recently, new paradigms are emerging that offer accounts for how effort can be both avoided and valued at different points in time [130]. For example, when people are under pressure to exert effort to meet a deadline, neural correlates of this 'pressure' have been found in sub regions of the putamen and mid-cingulate cortex (MCC) that lead to a switch in the value of effort from cost to benefit [131]. Thus, the future of effort-based decision-making research may lie in understanding the situations and computations underlying when effort is not treated as a cost.

6.0 Conclusion

Every day we make decisions about whether to exert effort to obtain rewards, persist and motivate behaviours over extended periods of time, and adapt our decisions of whether to exert effort due to changes in our bodies, brains, and the external environment. Computational models have helped us identify the hidden neural mechanisms underlying multiple aspects of effort-based choice, including how people discount reward by effort, learn about effort over time, or how fatigue influences the motivation to exert effort. Research has identified a dopamine driven fronto-striatal circuit, that seems to play a central role in deciding whether to exert effort, controlling our behaviours when we exert ourselves, and updating our motivation over time. Disruptions to this circuit are linked to variability in motivation in healthy people and in disease. Yet there is much still to learn. Future advances will come from research offering new theories of motivation beyond the law of less effort, and integrating methods and knowledge across ecology, neuroscience and economics. Such efforts may bring us closer to understanding why we sometimes think hard work isn't 'worth it'.

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