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Searching for Worth: The Impact of Effort Throughout Reward Processing

Paula López-Gamundí

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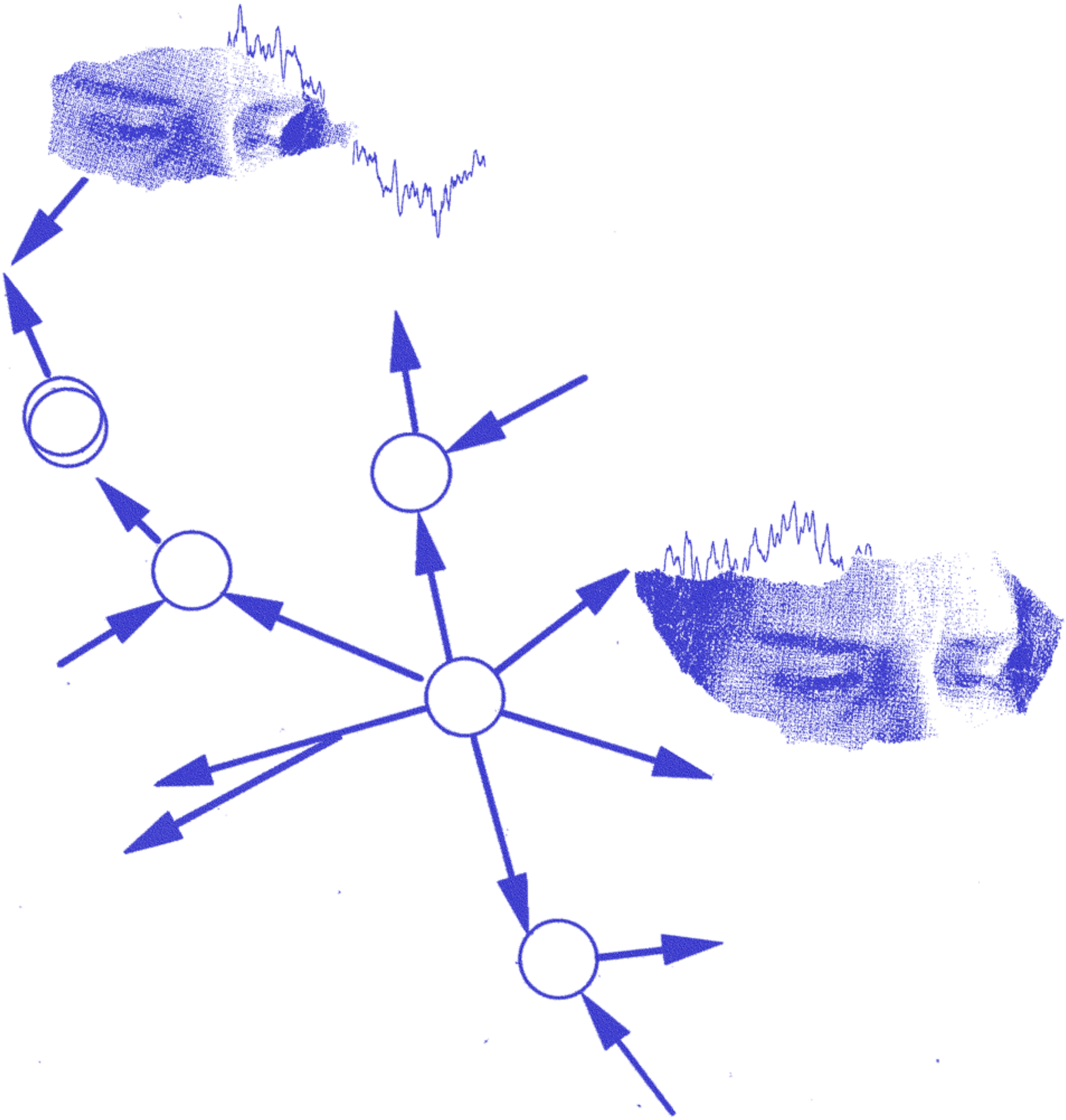
SEARCHING FOR WORTH

the impact of effort throughout reward processing



Paula López-Gamundí

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Paula López-Gamundí

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Dr. Josep Marco Pallarés
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Contents

Abstract

What drives behavior? This fundamental inquiry has been the cornerstone of disciplines spanning from philosophy to biology. In neuroscience and economics, however, the prevailing viewpoint posits that reward plays a central role in motivating an organism's behavior, such that one is willing to endure larger costs for more valuable rewards. Within this framework, effort naturally becomes an integral component of reward valuation since the subjective value of a reward can be observed through the level of effort one is willing to expend to obtain it.

Despite the inherent connection between effort and reward, the impact that effort costs have on reward value – and the neural architecture that underlies that valuation process – remains unclear. Extant research indicates that the processing of effort sometimes occurs in the same brain regions as other cost-based rewards, while at other times, it engages distinct prefrontal regions, suggesting that effort demands are treated separately from other reward-related costs. Additionally, substantial evidence suggests that effort requirements diminish the value of prospective rewards, as demonstrated by the consistent preference of animals and humans for pursuing less effortful rewards. Interestingly, this preference reverses once a reward is obtained such that more value is attributed to rewards earned through greater effort. This dissociation presents a unique opportunity to explore how effort and reward are integrated during reward receipt and incorporated into representations of future predicted rewards. Nevertheless, previous studies tend to focus on select phases of effort-based reward processing in isolation, obscuring a fuller understanding of this valuation process. This factor, coupled with variability in experimental paradigms and insufficient control for confounders like success probability, potentially contribute to inconsistencies in previous findings, necessitating new research focusing on how pure effort demand impacts reward processing.

In this thesis, we employed a diverse range of techniques to examine the influence of effort costs at different stages of reward processing. Firstly, we conducted a comprehensive meta-analysis, utilizing both coordinate-based and image-based approaches to identify brain regions consistently involved in signaling prospective effort demands and the net value of effort-based rewards. Our findings indicate that during the evaluation and selection of cues, the net value of effort-based rewards is represented by a system comprised of the ventromedial prefrontal cortex (vmPFC) and the ventral striatum, regions known to play a role in processing the subjective value of rewards across various domains, costs, and stages of processing. The meta-analysis also revealed a specific role for the pre-sensory motor area (pre-SMA), which tracked both effort costs and net value, albeit in a different manner than the vmPFC. These results provide robust evidence for the distinct contributions of the vmPFC and pre-SMA in valuing incentivized effort

costs and highlight their central involvement in the network that drives motivated behavior.

While preparing the meta-analysis, we observed that many experimental designs included features that generated confounds that could have potentially contributed to conflicting findings from previous studies. Motivated by this observation, we aimed to design a simple experimental paradigm that would allow us to isolate pure effort and reward value signals by controlling critical confounding factors, measuring responses across different phases of reward processing, and assessing effort-based reward signals in the absence of option comparison. Surprisingly, across two experiments, we failed to observe any net value signal during cue evaluation at the pre-SMA/dACC (as putatively measured by frontal midline theta). Instead, effects in component P3 suggest that higher magnitude and less probable rewards were more salient than lower magnitude and more probable rewards, and that paid effort costs amplified this effect. Additionally, we observed enhanced theta power for successful high effort outcomes, although theta did not track reward magnitude. These findings suggest that the pre-SMA/dACC does not track prospective effort when success rates are equivalent between effort conditions and in the absence of option comparison. Finally, effort-related effects at feedback indicate that rewards earned through high effort are more salient, suggesting a general attentional bias toward high effort outcomes.

We next aimed to test whether this attentional bias could potentially modulate individuals learning speed. Specifically, we were interested in exploring how cognitive effort modulates the reinforcing value of received rewards. Our results indicated that participants successfully acquired cue-reward contingencies but that learning rates were unaffected by effort demands. Instead, we observed an effect of performance feedback, such that learning rates were higher when participants successfully completed the effort task than when efforts were unsuccessful.

Collectively, the findings presented in this thesis provide several crucial insights into the field of effort-based reward processing. Firstly, we provide compelling evidence that the net value of prospective effort-based rewards engages a system involving the vmPFC and pre-SMA, with supporting roles played by the ventral striatum, anterior cingulate cortex, and anterior insula. This suggests that effort is treated similarly to other costs within the framework of value-based decision-making. Furthermore, we demonstrate that when reward probabilities are fully dissociated from effort requirements, frontal midline theta primarily reflects expended effort during reward delivery and that effort enhances the salience of rewards during feedback, which suggests that more attention is allocated to rewards obtained through greater effort. Lastly, we investigated the impact of cognitive effort demands on reward learning and found that positive performance feedback, but not effort demands, facilitated the updating of cue-reward contingencies.

In conclusion, this thesis significantly advances our understanding of effort-based reward valuation by shedding light on the neural mechanisms involved at different stages of reward processing. This collection of work provides conclusive evidence for the roles of the vmPFC and pre-SMA in valuing prospective incentivized effort costs. The current findings also provide additional evidence in support of the idea that effort is weighed differently in early stages of reward processing (i.e., choice, cue evaluation, etc.) than in later stages (i.e. feedback, learning, etc.) and that performance feedback may be more relevant in certain contexts than sheer effort expen-

diture. Critically, these findings also underscore the need to reevaluate current methodologies in the field of neuroeconomics, as the failure to replicate certain established effects calls for a comprehensive reevaluation of existing practices.

keywords: effort, reward processing, subjective value, medial prefrontal cortex (mPFC), frontal midline theta (FMT), effort-based reward, motivation

Resumen

¿Qué impulsa el comportamiento? Esta pregunta fundamental ha sido el pilar de diversas disciplinas, desde la filosofía hasta la biología. En neurociencia y economía, la perspectiva predominante propone que la recompensa es uno de los principales impulsores del comportamiento del organismo y que estamos dispuestos a invertir más esfuerzo por recompensas de mayor valor. Según esta lógica, el esfuerzo es un componente natural de la recompensa, ya que el valor subjetivo de una recompensa puede observarse en el grado de esfuerzo que uno invierte para obtenerla.

A pesar de la relación clara entre el esfuerzo y la recompensa, existen aún grandes lagunas en nuestro conocimiento sobre como el esfuerzo afecta el valor de la recompensa. Hallazgos de experimentos de neuroimagen indican que a veces el esfuerzo se procesa en las mismas regiones del cerebro que otros costes, pero otras veces se procesa en regiones completamente diferentes. También tenemos evidencia significativa de que las demandas de esfuerzo reducen el valor de las recompensas futuras, como se evidencia en la observación consistente de que animales y humanos prefieren buscar recompensas que requieran menos esfuerzo. Sin embargo, curiosamente, una vez que se obtiene una recompensa, esta relación se invierte y las recompensas que fueron conseguidos tras mayor esfuerzo tienden a ser más valoradas. Esta disociación nos brinda una oportunidad única para observar cómo se integra el coste de esfuerzo al valor de una recompensa antes y después de ejercer ese esfuerzo, y cómo se incorporan estas representaciones en las predicciones de recompensas futuras. Sin embargo, los estudios anteriores tienden a centrarse, de forma aislada, en fases selectas del procesamiento de recompensas, lo cual limita una comprensión más completa del proceso de valoración. Junto con diferencias entre paradigmas experimentales y la falta de control de factores de confusión como la probabilidad de éxito, estos factores potencialmente contribuyen a las inconsistencias en los hallazgos anteriores, lo cual impulsa nuevas investigaciónes que puedan captar el efecto de esfuerzo en representaciones de la recompensa.

En esta tesis se ha utilizado un conjunto diverso de técnicas para investigar el impacto del esfuerzo en diferentes etapas del procesamiento de la recompensa. En primer lugar, realizamos un metaanálisis híbrido basado en coordenadas e imágenes para identificar las regiones consistentemente involucradas en la señalización de las demandas prospectivas de esfuerzo y el valor neto de las recompensas basadas en el esfuerzo. Nuestros hallazgos sugieren que durante la evaluación y elección de las señales, el valor de las recompensas basadas en el esfuerzo se representa en un sistema compuesto por la corteza prefrontal ventromedial (vmPFC) y el cuerpo estriado ventral, regiones implicadas en el procesamiento del valor subjetivo de las recompensas

en diversos dominios y con diversos costes. El metaanálisis también reveló un papel especial para el área motora pre-sensorial (pre-SMA), que seguía tanto los costes del esfuerzo como el valor neto, aunque con efectos opuestos a las que fueron identificadas en el vmPFC. Estos resultados proporcionan evidencia sólida sobre el papel diferenciable del vmPFC y el pre-SMA en la valoración de los costes del esfuerzo incentivado, y muestran que estas dos regiones son actores centrales en la red que impulsa el comportamiento motivado.

Al revisar los datos del metaanálisis, observamos varias diferencias importantes en los diseños experimentales, lo cual limitaba la interpretación de los hallazgos. Esto nos llevó a intentar aislar las señales puras de esfuerzo y valor de recompensa mediante la creación de un paradigma que nos permitiera: 1) controlar factores críticos de confusión, 2) medir las respuestas en diferentes fases del procesamiento de la recompensa y 3) medir las señales de recompensa basadas en el esfuerzo sin tener que comparar opciones. Sorprendentemente, en dos experimentos no logramos encontrar ninguna señal de valor neto en la evaluación de las señales. Por el contrario, los efectos en el componente P3 sugieren que las recompensas de mayor magnitud y menos probables resultaron más salientes que las recompensas de menor magnitud y más probables, y que los costes del esfuerzo amplificaron este efecto. Además, observamos un aumento en la potencia de la onda theta para los resultados exitosos de alto esfuerzo, aunque dicha actividad no correlacionó con la magnitud de la recompensa. Estos hallazgos sugieren que el preSMA/dACC no sigue el esfuerzo prospectivo cuando las tasas de éxito son equivalentes entre las condiciones de esfuerzo y en ausencia de comparación de opciones. Por último, los efectos relacionados con el esfuerzo en la retroalimentación indican que las recompensas obtenidas a través de un alto esfuerzo son más relevantes, lo que sugiere un sesgo de atención general hacia los resultados de alto esfuerzo.

La ausencia de una señal de valor neto en la evaluación de las señales nos llevó a cuestionar la relevancia del valor neto en esta fase bajo condiciones en las cual el esfuerzo era obligatorio y las probabilidades de recompensa eran comparables entre diferentes niveles de esfuerzo. En su lugar, planteamos la hipótesis de que la entrega de recompensa podría ser más relevante, ya que el esfuerzo y los resultados de recompensa podrían proporcionar más información sobre el valor de una opción determinada. Por lo tanto, nos propusimos explorar si el esfuerzo cognitivo modula el valor reforzante de una recompensa recibida. Nuestros resultados indicaron que los participantes adquirieron exitosamente las contingencias estímulo-recompensa, pero que la tasa de aprendizaje no se vio afectada por las demandas de esfuerzo. Sin embargo, observamos un efecto del retroalimentación de rendimiento, ya que las tasas de aprendizaje fueron más altas cuando los participantes recibieron retroalimentación positivo.

En conjunto, los hallazgos de esta tesis contribuyen al campo del procesamiento de recompensas basado en el esfuerzo de varias maneras cruciales. En primer lugar, proporcionamos las primeras pruebas concluyentes de que el valor neto de las recompensas prospectivas basadas en el esfuerzo recluta un sistema compuesto por la vmPFC y el pre-SMA, con papeles de apoyo desempeñados por el estriado ventral, la corteza cingulada anterior y la ínsula anterior. Esto sugiere que el esfuerzo se trata de manera similar a otros costes dentro del marco de la toma de decisiones basada en el valor. Además, demostramos que cuando las probabilidades de recompensa se desvinculan por completo de los requisitos de esfuerzo, la amplitud theta en la línea media frontal refleja principalmente el esfuerzo invertido durante la entrega de la recompensa,

y que el esfuerzo realza la relevancia de las recompensas durante el feedback, lo que contradice la noción de que las recompensas obtenidas con mayor esfuerzo pierden valor. Por último, investigamos el impacto de las demandas de esfuerzo en el aprendizaje de recompensas y encontramos que el feedback positivo, pero no las demandas de esfuerzo, facilita la actualización de las contingencias estímulo-recompensa.

En conclusión, esta tesis avanza significativamente nuestra comprensión del procesamiento de recompensas basado en el esfuerzo. Este conjunto de investigaciones proporciona evidencia concluyente sobre las funciones de la vmPFC y el pre-SMA en la valoración de los costes prospectivos incentivados del esfuerzo. Además, los hallazgos actuales respaldan la idea de que el esfuerzo se evalúa de manera diferente en las etapas iniciales del procesamiento de la recompensa (elección, evaluación de señales, etc.) que en las etapas posteriores (feedback, aprendizaje, etc.), y que el feedback de rendimiento puede ser más relevante en ciertos contextos que el simple esfuerzo. Es importante destacar que estos hallazgos también subrayan la necesidad de reevaluar las metodologías actuales en el campo de la neuroeconomía, ya que la falta de replicación de ciertos efectos establecidos requiere una revisión crítica de las prácticas existentes.

palabras claves: esfuerzo, procesamiento de recompensas, valor subjetivo, corteza prefrontal medial (mPFC), theta de línea media frontal (FMT), recompensa basada en el esfuerzo, motivación

Chapter 1

Introduction

How organisms organize their behavior to reach a goal is one of the fundamental dilemmas of value-based decision-making. Critically, goals and rewards are generally obtained by exerting directed effort and this effort plays a crucial role in how that reward is evaluated. The study of effort-based reward processing has yielded valuable insights into the behavioral patterns and associated underlying neural mechanisms of reward and effort valuation. However, findings are inconsistent and oftentimes contradictory and further investigation is needed to elucidate the precise impact of effort expenditure on reward value, as well as the factors that modulate this relationship. This thesis employs a variety of approaches, integrating neuroimaging techniques and novel behavioral paradigms, with the aim of unraveling the intricate interplay between effort expenditure and reward value.

In order to understand the effect of effort on reward value, it is first necessary to understand the theoretical frameworks of reward valuation and the neural architecture supporting this process. In the following sections, we will provide a basic overview of reward processing as a whole, how effort costs are integrated into this valuation process, and how the subjective value of effort-based rewards are measured.

1.1 Defining Reward Value

To study reward we must first understand how reward is defined. Rewards can be intrinsic (e.g., satisfaction) or extrinsic (e.g., an award). Rewards can also be primary, or essential for survival (e.g., food), or secondary (e.g., money, social inclusion) in nature. However, for an option to be deemed rewarding, it must have some concept of value. The value of reward cannot be measured directly and is instead estimated from observable behavior. The most intuitive feature of reward value is the hedonic pleasure one experiences when consuming a reward. The hedonic response to a reward is generally referred to as “liking” (Berridge et al., 2009; Schultz, 2015). Importantly, the value of a reward is directly related to the degree that is liked, such that higher value is assigned to rewards that induce more pleasure. Liking is often measured using physiological responses, such as electromyography facial recordings and skin conductance arousal. Reward liking can also be measured behaviorally. For example; rats emit squeaks when presented with appetitive rewards and both animals and humans lick their lips in response to sweet, but not bitter, tastes (Berridge and Kringelbach, 2015). However, early studies of reward pleasure astutely observed that pleasure is not only passively experienced, but it is also sought out. Specifically, Olds and Milner (1954) observed that electrical stimulation of specific brain regions in rats had a “rewarding effect” such that, given the option to control stimulation (via lever press in a Skinner box), rats would repeatedly press a lever to self-administer stimulation. Thus, stimulating certain brain regions provided a reinforcing effect (Olds and Milner, 1954), suggesting that hedonic response to external rewards is not the only factor which underlies reward value.

This highlights another important feature of reward value: approach behavior. The incentive motivation that promotes approach towards rewards is generally referred to as “wanting” (Berridge et al., 2009; Schultz, 2015). In neuroscience, psychology, and behavioral economics alike, value is often operationalized by the level of investment one is willing to make to obtain that reward, such that organisms prefer and more vigorously pursue more valuable rewards. For example, decades of research has shown that rewards that induce more pleasure are more vigorously pursued than their less pleasurable alternatives (Salamone et al., 2018). Thus, wanting – and its behavioral correlates – can also be used as an indicator of value itself.

Finally, reward value can be altered by a variety of contextual factors, such as internal or external states (e.g. food is more valuable when hungry than when satiated, change in food sources, etc.). Thus, the value of rewards are not static, but are malleable and dependent on environmental factors. To adapt to changes in the environment, reward values, and the actions taken to pursue them, must be tracked and updated. This brings us to the third function of reward value: learning (Berridge et al., 2009; Schultz, 2015). Reinforcement learning is defined as the process by which associations between actions and rewarding outcomes are established and how predictions and behaviors are adjusted when outcomes differ from expectations (Schultz, 2016). This learning process implicitly relies on some representation of value, since generating predictions about future rewards based on past experiences requires the comparison of current reward value estimates with previous value estimates (Schultz, 2016).

1.2 The When, Where, and How of Reward Value

The wanting and learning functions of reward are distinct from liking not only in their nature, but also in their temporality. While liking refers to the hedonic experience of receiving a reward, wanting and learning imply a desire for and a prediction of a reward before it occurs. These functions would require a representation of reward value prior to delivery. This phase in reward processing is generally referred to as reward anticipation and includes not only the hedonic impact of expecting a reward, but also the predicted value of that reward (Assadi et al., 2009; Webber et al., 2020).

1.2.1 Signaling Reward Before It Occurs

Neural activations associated with reward anticipation were first studied under the scope of Pavlovian conditioning. Under these paradigms, an arbitrary stimulus (conditioned stimulus, CS) with no inherent reward properties (i.e. light flash, sound beep) is systematically and reliably presented before a reward (unconditioned stimulus, UCS). Over time, an association between the stimulus and the reward is developed such that the CS becomes predictive of the UCS (Mackintosh, 1994). As this predictive association develops, rewarding responses begin to not only occur at reward consumption, but also in anticipation of a reward. The first neuronal activity during reward anticipation was reported by Miller et al. (1981), who identified dopamine responses to conditioned light in rats treated with haloperidol. In the decades that followed, seminal work by Schultz et al. (1998, 1997) revealed how dopaminergic neurons in the ventral tegmental area (VTA) signal anticipated or predicted rewards. As shown in Figure 1.1A, the firing rate of dopaminergic neurons in the VTA increases when receiving the UCS, initially encoding for reward delivery. However, as the contingency between CS and UCS is developed, VTA neural firing will shift towards the predictive stimulus (Figure 1.1B). Critically, once the association is fully acquired, DA neurons in the VTA no longer respond to reward delivery. Instead, dopamine neurons in the VTA will respond to rewards only when their delivery differs from the learned prediction. For example, dopamine firing is suppressed when an expected reward is omitted (Figure 1.1C). Conversely, firing rate increases when rewards are suddenly delivered earlier or later, or are of a different magnitude than predicted (Schultz et al., 2015). This sensitivity to the predictability of reward outcomes suggests that dopamine neurons in

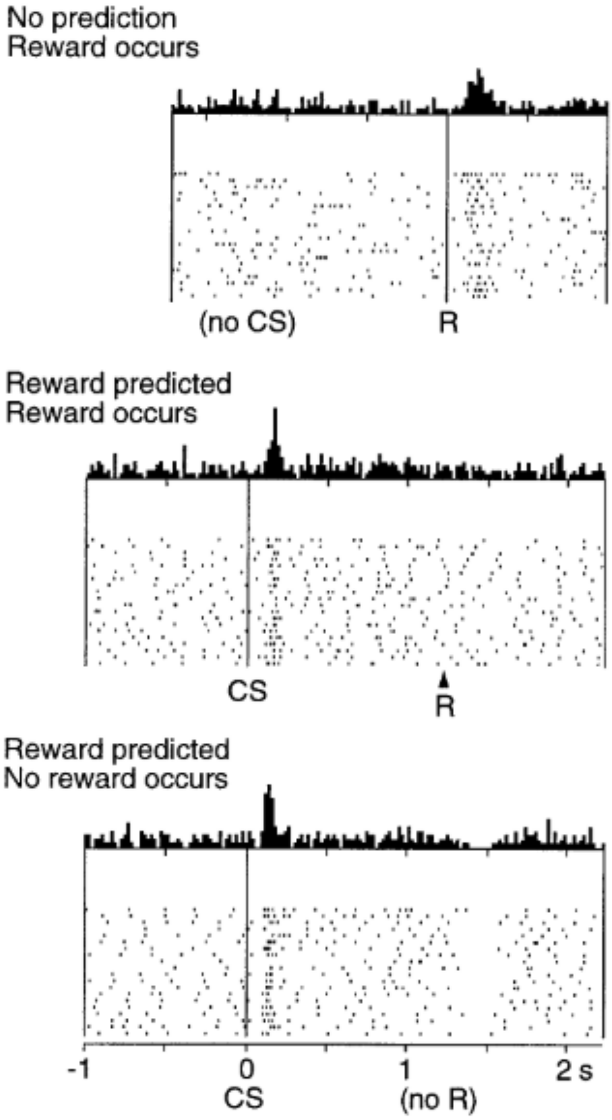

Figure 1.1: Schematic of DA neuron firing in the VTA. Top figure show firing in response to reward delivery (R). Middle figure shows DA shift in firing towards the condition stimuli (CS) after acquisition of cue-reward association. Bottom figures shows suppression of DA neurons when predicted reward is omitted (no R). Adapted from Schultz et al. (1997)

the VTA do not encode the hedonic properties of a reward, but rather encode features of the stimulus-reward contingency. Further, they confirm the existence of neural representation of anticipated and predicted reward and directly implicate midbrain dopamine in this signaling at both cue and feedback.

1.2.2 Neuroanatomy and Electrophysiological Activity Implicated in Reward Value and Prediction

Since then, considerable effort has been dedicated to elucidating how VTA-DA input to cortical and subcortical brain areas contributes to neural encoding of value and reward prediction. Over the years, a general reward pathway has been identified. This pathway is primarily composed of brain regions in the cortico-basal ganglia loop, with key hubs in the VTA / substantia nigra (SN) and ventral striatum (VS), but also other key structures such as the amygdala, ventral pallidum (VP), insula, anterior cingulate cortex (ACC), ventromedial prefrontal cortex (vmPFC) and orbitofrontal cortex (OFC). Through a complex interaction of dopaminergic, GABAergic, and opioidergic pathways, this system is activated for rewards across all domains and modalities (Bartra et al., 2013; Mas-Herrero et al., 2021; Sescousse et al., 2013), and throughout all stages of reward processing (Bartra et al., 2013; Berridge and Kringelbach, 2008; Chase et al., 2015). Of key interest is the transmission of dopamine through three main pathways. Thus, it is worthwhile to briefly review the DA receptor types and signaling dynamics in the reward circuitry before discussing where specific aspects of reward value are represented in the brain. Finally, we will also review general concepts of neural electrophysiology and what neuronal activity at the population level is thought to be involved in reward processing.

1.2.2.1 Dopamine Receptor Types and Signaling Dynamics

Midbrain DA has two types of signaling behaviors: phasic and tonic. Phasic activity, or "burst firing", refers to a rapid series of action potentials that release large concentrations of DA (Floresco et al., 2003; Grace, 1991; Grace, 2000). Conversely, tonic activity refers to steady-state, single spike firing, which slowly diffuses and raises levels of extracellular DA (Floresco et al., 2003; Grace, 1991; Grace, 2000). However, not all DA receptors are sensitive enough to react to low, tonic levels of DA. So far, five different DA receptor types have been identified, labeled D1-D5. These receptors are generally categorized into two families: D1-like receptors, which include D1 and D5, and D2-like receptors, which include D2, D3, and D4. These subtypes differ in their G-protein coupling and affinity and are also distributed across synapses and brain regions in different concentrations. For example, D1-like receptors are mostly present pre-synaptically and are abundant in the PFC, striatum, NAcc, and olfactory tubercle. Meanwhile, D2-like receptors are present pre- and post-synaptically and are more highly concentrated in the striatum. Critically, D2-like receptors have much higher affinity than D1-like receptors and can be stimulated in low-DA states. Thus, D2-like receptors are more likely to be activated by tonic levels of DA, whereas D1-like receptors require higher concentrations of DA release and are thus stimulated by phasic DA activity.

DA neurons originating in the VTA/SN project along three ascending pathways (Figure 1.2). Terminating in the dorsal striatum (dorsal caudate and putamen), the nigrostriatal pathway is generally implicated in motor control and habit learning (Bourdy et al., 2014; Faure et al.,

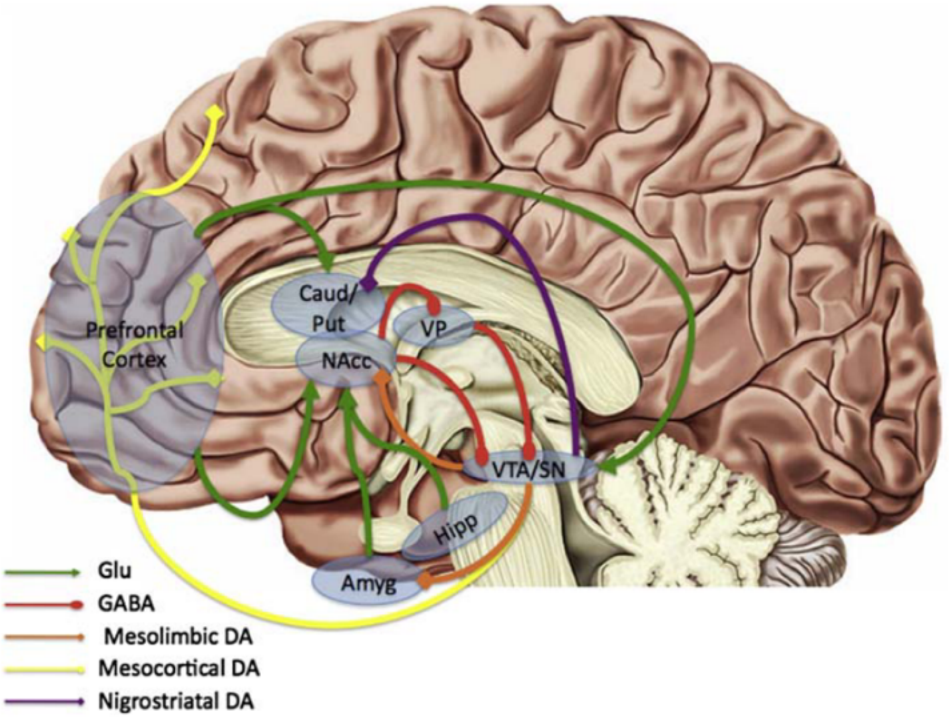

Figure 1.2: Schematic illustration of reward circuit, and the glutaminergic (Glu), GABAergic (GABA), and dopaminergic (DA) pathways linking the different regions. **Amyg**, amygdala; **Caud**, caudate; **Hipp**, hippocampus; **NAcc**, nucleus accumbens; **Put**, putamen; **SN**, substantia nigra; **VP**, ventral pallidum; **VTA**, ventral tegmental area. Adapted from Treadway and Zald (2011).

2005; Redgrave et al., 2010). The mesolimbic pathway has terminals in the VS, amygdala, and hippocampus, and has been linked to reinforcement learning and motivational components of reward (Salamone and Correa, 2012; Salamone et al., 2016). The mesocortical pathway projects to terminals in cortical regions, such as the ACC, mPFC, OFC, and insula, and has been implicated in a variety of functions that subserve wanting, such as working memory, attention, and cognitive control (Floresco and Magyar, 2006; Wise, 2005).

These three pathways, especially the mesolimbic and mesocortical pathways, are generally referred to as the "reward circuit", since several aspects of reward anticipation and outcome processing have been linked to the complex interplay between dopamine (as well as other neurotransmitters) projections from the basal ganglia to cortical target regions (Haber and Knutson, 2010). Thus, although many aspects of reward are modulated by subcortical structures, measures of cortical activity, including electrophysiological signatures of this activity, are also highly informative of the cognitive and neural processes underlying reward value and goal-directed behavior.

1.2.2.2 Electrophysiological Components Relevant to Value Processing.

When neurons fire, they produce an electrical signal. This electrical activity can be categorized into action potentials and postsynaptic potentials. Action potentials occur when a target neuron receives sufficient input from an excitatory neuron so that it depolarizes and fires a discrete voltage spike. This action potential originates in the cell body and is propagated through to the axon terminals where neurotransmitters are released. Conversely, postsynaptic potentials are the voltages that arise when the neurotransmitters bind to receptors on the postsynaptic terminal, resulting in graded change in voltage across the cell membrane. The summation of the postsynaptic potential activity of a neural population can be captured by recording the local field potential. These field potentials of cortical pyramidal cells are recordable from the scalp using electroencephalography (EEG) techniques.

The electrical signals recorded from neuronal ensembles can be analyzed in several ways, but one of the most common indices is event-related potentials (ERPs). ERPs refer to variations in voltage that are time-locked to a sensory or cognitive event. While ERPs vary in their time-course, scalp topographies, and distinct cognitive functions, several have been identified as relevant to reward processing. For example, two ERP components – the cue-N2 and the cue-P3 – appear to be reliably sensitive to features of cues indicating upcoming rewards. Specifically, the cue-N2 is a negative-going fronto-central ERP that arises 200-300ms after cue onset which has been hypothesized to signal either upcoming cognitive control demands or a violation of expectations (template mismatch; Glazer et al., 2018; Luck, 2014). Occurring a bit later (300-600ms after cue onset) and in more parietal sites, the positive-going cue-P3 is hypothesized to signal the saliency of a cue. Because it is modulated by likelihood and reward magnitude, cue-P3 is usually interpreted as indexing motivated attention for reward-predictive cues (Glazer et al., 2018; Luck, 2014). Similar ERP components appear at reward delivery or feedback, however these components represent unique, albeit somewhat comparable, processes at different timepoints. The feedback-related negativity (FRN) is a variation of the N2-family; it is a fronto-central ERP component thought to be generated in the mPFC (Cohen et al., 2007; Foti et al., 2015), which peaks about 200 to 300ms following feedback onset. The FRN is not consistently related to reward magnitude, but it is reliably sensitive to performance evaluation and reward likelihood, and is generally larger for negative than positive feedback and for unlikely than likely positive feedback, making it a candidate neural marker for prediction error signaling (Glazer et al., 2018; Luck, 2014; Sambrook and Goslin, 2015). However, researchers have also observed that the magnitude of the FRN is driven more by a positive-going deflection elicited by reward-related response as opposed to a negative deflection elicited by an error-related response (Krigolson, 2018). This reward-specific activation has been deemed the Reward Positivity (RewP; Holroyd et al., 2011; Holroyd et al., 2008). It is more central than the loss-related FRN and has been shown to be generated in the ACC/mPFC and striatum (Becker et al., 2014; Foti et al., 2011). Like the FRN, RewP amplitudes are modulated by reward prediction violation and outcome probabilities (Bernat et al., 2015; Hajcak et al., 2007; Sambrook and Goslin, 2015). In contrast, the feedback P3 (fb-P3) is sensitive to other properties of reward feedback, such as magnitude and probability, but does not appear to reflect performance evaluation. This positive-going, centro-parietal deflection peaks from 300 to 600ms post feedback onset and is thought to reflect resource allocation and motivational salience (Glazer et al., 2018; Luck, 2014).

In addition to looking at temporal variations of voltage, as is done with ERP components, EEG signals can also be quantified by looking at the amplitude of deflection in the frequency domain. This measure is referred to as time-frequency power and allows researchers to capture both phase-locked (called evoked power) and out-of-phase (called induced power) oscillatory activity, the latter of which is lost in an averaged ERP waveform. Time-frequency components are defined by their time-course and frequency band. Although there is some variability in frequency ranges, the canonical frequency bands are delta (1-3 Hz), theta (4-7 Hz), alpha (8-12 Hz), beta (13-25 Hz) and gamma (26-80 Hz) (Cohen, 2014; Luck, 2014). Of these frequency bands, beta and theta are particularly relevant for reward anticipation and feedback processing. Beta power is typically measured in fronto-central midline sites about 200-600ms following stimulus onset (Luft, 2014). It has been hypothesized that beta activity promotes incentive-motivational processes, since studies have shown that beta power is enhanced for reward-predictive cues and that beta suppression during motor-preparation facilitates behavioral approach (Glazer et al., 2018). At outcome, beta power is also linked to reward and performance feedback processing and has been proposed as a candidate signal for motivated learning (Marco-Pallares et al., 2008; Marco-Pallarés et al., 2015). Theta power is also measured at frontal-midline sites, however in the context of reward processing it is typically looked at during outcome, where it generally peaks from 200 to 500ms post feedback onset (Glazer et al., 2018). Frontal midline theta has been shown to be sensitive to both reward and feedback evaluation (Bernat et al., 2015; Hajihosseini and Holroyd, 2013) and related to behavioral adjustment (Cavanagh and Shackman, 2015) and learning rate (Mas-Herrero and Marco-Pallarés, 2014). More recently however, there has been more interest in the role of theta during reward anticipation, especially in relation to the allocation of cognitive control for goal-directed behavior (Cavanagh and Frank, 2014; Verguts, 2017). This is critical, as we see that the direction and intensity of goal-directed behavior is directly influenced by costs associated with a given reward.

Taken together, these ERP and time-frequency components provide valuable insight into the cognitive and neural mechanisms underlying reward processing in humans and are candidate measures for investigating the impact of effort costs on neural signatures of reward value.

1.3 When Reward Comes at a Cost

Anticipating a reward inherently implies a representation of this future reward and the relevant environmental features associated with obtaining it (Rangel et al., 2008). These environmental features include external and internal states which can influence how that reward is valued. For example, one million dollars are valued differently when you have a low probability of winning them (e.g. as in a lottery) versus when you have total certainty that you will be paid. Similarly, food does not have the same value when you are full as when you are starving. Thus, to understand reward value, one must also explore relevant features that can influence this valuation process.

Researchers in behavioral economics have been traditionally concerned with decision-making processes, particularly in how costs associated with certain rewards drive economic choice. This framework lent itself well to behavioral and affective neuroscience since choice behavior provides a reliable behavioral correlate of the emotional and subjective value of a reward. These fields naturally intersected, forming what is now known as neuroeconomics. Despite the diversity of mechanistic and theoretical perspectives in this field, all theories of neuroeconomics posit that motivated, or goal-directed, behavior is driven by cost/benefit trade-offs (Salamone et al., 2018; Westbrook and Braver, 2015; Zald and Treadway, 2017). In this valuation process, expected costs are weighed against predicted benefits, resulting in a net value (also referred to as the subjective value or decision value) of an option. The definition of benefits used in neuroeconomics overlaps greatly with our prior definition of reward and can be primary or secondary, as well as internal or external in nature. Costs also depend on internal and external states and, although there are a variety cost types, the costs most discussed in the literature are temporal delay, probability of reward, and effort required to obtain a reward (Bailey et al., 2016; Rangel et al., 2008). The mechanism by which costs and benefits are integrated to derive net value remains a topic of active debate (Kolling et al., 2016; Rangel et al., 2008; Shenhav et al., 2013; Vassena, Holroyd, et al., 2017). However, most neuroeconomic theories agree that net values provides a "common currency" by which options can be equally compared, thereby guiding choice and action selection (Padoa-Schioppa, 2011).

In economics, one way of finding the subjective reward value of an item is to simply find the maximum amount one is willing to pay to obtain it. Under the neuroeconomics framework, this perspective has been broadened to include willingness to endure any type of cost in order to obtain said reward. The most common external costs studied are probability, delay, and effort, although others like efficacy and opportunity costs have been explored (Bailey et al., 2016; Frömer et al., 2019; Shenhav et al., 2021). Based on extensive behavioral findings in both animals and humans, these costs are assumed to discount the value of a reward, such that rewards that are less probable, more delayed, or require more effort to obtain are preferred less than their more probable, more immediate, or less effortful alternatives (Salamone et al., 2018; Zald and Treadway, 2017). These findings are primarily based on paradigms that utilize a neuroeconomic framework to study cost-benefit weighting. Since the focus of this dissertation is on the effect of effort on reward value, we will limit the scope of this review to paradigms which use effort as a response cost.

1.3.1 Measuring Net Value

One of the prominent paradigms that has been used to assess the impact of effort demand on reward preference is the T-maze barrier choice procedure developed by Salamone et al. (1994). In this procedure, one arm of the maze contains a small amount of food while the other arm contains a larger amount of food with a vertical barrier in front. Rodents must therefore climb over the barrier to get the larger reward (see Figure 1.3A). Healthy rodents will generally go over the barrier to get to the larger food reward. When both arms have the same amount of food, however, animals will avoid effort and prefer the arm with no barrier. Thus animals are effort avoidant, unless reward is a function of more effort (Salamone and Correa, 2012; Salamone et al., 2018).

Another commonly used task for assessing effort-based choice in animals is the concurrent lever-pressing procedure, also developed by Salamone and colleagues (1991). In this paradigm, rodents are given the choice between either lever pressing to obtain a relatively preferred food or approaching and consuming a less preferred food (lab chow) that is concurrently available in the chamber. Under baseline conditions, rodents typically prefer lever pressing and only consume small quantities of lab chow, again showing preference to endure effort when rewards are sufficiently salient.

These procedures were directly translated to humans (Salamone et al., 2018; D. H. Treadway,

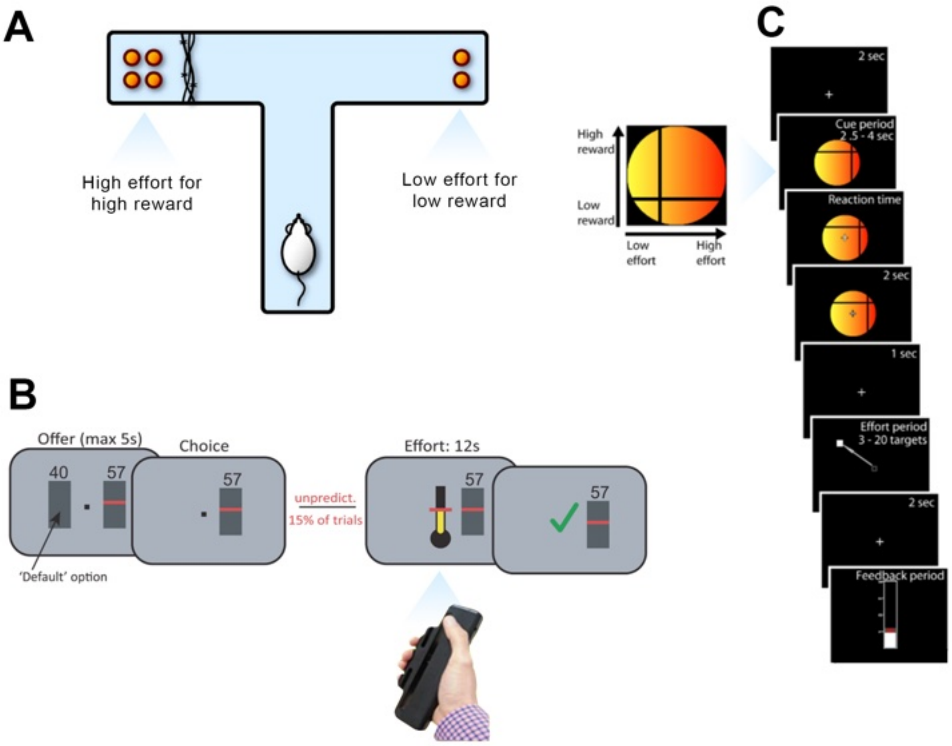

Figure 1.3: Examples of common effort-based reward paradigms. **(A)** T-maze barrier choice paradigms. Rodents freely choose between climbing a barrier for a preferred food (high effort for high reward) or a less preferred food with a smaller or no barrier (low effort for low reward). **(B)** Dual-alternative effort-based decision-making paradigm. Participants are given a maximum of 5 seconds to choose between a default option (40 pence with no effort) and another option with higher effort requirements, but also higher payoffs (55% of maximum voluntary contraction for 57 pence). Participants then exert the force for 15% of their selections. In this case, they must reach the grip threshold and hold for 12 seconds. Reward is only given if effort is correctly exerted. **(C)** Passive effort-based reward task. In this task by (Croxson et al., 2009), participants are presented with a compound effort and reward cue. Participants then have two seconds to emit a button response before having to complete a trackball task of varying degrees of difficulty (ranging from 8 targets at the lowest level of effort and 20 targets at the highest level of effort). Feedback about the amount of reward gained on the trial is then presented. Image A has been adapted from Assadi et al., (2009), B from Klein-Flügge et al., (2015), and C from Croxson et al., (2009).

2011) and are analogous to T-maze and concurrent lever-pressing procedures. As seen in Figure 3B, dual-alternative paradigms in humans require subjects to repeatedly choose between a higher effort/higher reward option and a lower effort/lower reward option (Chong et al., 2016; Chong et al., 2015; Reddy et al., 2015). In some studies, the lower effort/lower reward alternative is simply a no effort/no reward option, and thus the participant only needs to accept or reject the offer on hand ("accept/reject tasks" in Chong et al., 2016). Irrespective of the format, these tasks produce estimates of net value by fitting choice data to discounting curves, which characterizes how reward is devalued as costs increases (Hartmann et al., 2015; Hartmann et al., 2013; Klein-Flugge et al., 2016). This procedure allows investigators to characterize the subjective, or net, value of an option based on an individual's personalized tolerance to expend effort to gain reward. Neural correlates of net value are then identified by employing neuroimaging techniques locked to the time of option presentation, or performing pharmacological manipulations to identify changes in choice behavior (Chong et al., 2016; Webber et al., 2020).

In addition to choice paradigms, there are also what we will call 1) progressive cost tasks and 2) passive tasks. In these paradigms, participants are not required to choose between two competing cost-benefit options. Instead, in “progressive cost” tasks, participants withstand increasing amounts of cost for higher rewards. The amount of cost incurred can be freely decided, and the putative measure of net value is the “breakpoint”, or the point at which the subject is unwilling to continue enduring a cost for a given reward value (Acheson and de Wit, 2008; Hershenberg et al., 2016). Finally, another group of studies have used “passive” cost-based reward paradigms, where participants are presented with a cue that signals the degree of cost and reward required to obtain an outcome (see Figure 1.3C). No choice is required in these tasks; however participants must endure the cost to obtain the reward. In these paradigms, neural correlates of subjective value are identified as brain activity that is sensitive to both reward and cost values near the time of cue presentation and reward delivery (Botvinick et al., 2009; Croxson et al., 2009).

The effort manipulations used in these paradigms can be broadly categorized into physical and cognitive tasks. Extant physical effort tasks used in humans include choice-based hand-grip tasks where willingness to exert effort is measured by motor force exerted on a grip (Clery-Melin et al., 2011; Kurniawan et al., 2010; Reddy et al., 2015; Schmidt et al., 2012) and choice-based or progressive cost button or lever pressing tasks (Hershenberg et al., 2016; Lane et al., 2005; M. T. Treadway et al., 2009). Running tasks have also been used in the context of exercise research, where preferences to run for less or more time in order to obtain less or more reward were fit to discounting models (Bernacer et al., 2016; Bernacer, Martinez-Valbuena, Martinez, Pujol, Luis, et al., 2019). Cognitive paradigms are substantially more varied and include Stroop tasks (Schmidt et al., 2012), cued set-switching tasks (Botvinick et al., 2009; Lopez-Gamundi and Wardle, 2018), visual shift tasks (Apps et al., 2015), memory search tasks (Ennis et al., 2013), attention tasks (Schevernels et al., 2014), backward typing of words (Massar et al., 2015), arithmetic tasks (Vassena, Silvetti, et al., 2014), and working memory tasks (Westbrook et al., 2013; Westbrook et al., 2019). These effort-based decision-making tasks generally either examine behavioral biases to avoid cognitive effort in choice-based tasks or are also used in discounting paradigms.

There is also a significant variety in the metrics used to analyze choice behavior in cost/benefit valuation tasks. Some tasks use percent of high effort choices to measure willingness to exert effort for reward (Barch et al., 2014; M. T. Treadway et al., 2009). Another approach is to use staircase paradigms in order to derive subject-specific effort indifference points (Klein-Flügge et al., 2015; Westbrook et al., 2013). The great majority of tasks however, use computational modeling based on discounting functions. As mentioned earlier, discounting curves are generally fit to trial-by-trial choices using a softmax function. These discounting functions take the reward value (R) of a given option on trial (t) and detract the cost (C) in order to calculate the subjective value (SV). Discounting functions can take various forms and are amendable to the specific parameters of a paradigm (Cooper et al., 2019; Soder et al., 2020), but the most popular are linear, hyperbolic, parabolic and exponential functions:

$$Linear : SV = R(t) * (1 - kE(t))$$

$$Hyperbolic: SV = R(t) * \frac{1}{kE(t)}$$

$$Parabolic: SV = R(t) - kE(t)^2$$

$$Exponential: SV = R(t) - e^{-kE(t)}$$

The discounting parameter k represents the steepness of each individual's discounting function. Thus, the higher the k value, the more an individual devalues a reward based on effort. Once a subject-specific discounting parameter is derived, trial-wise data can be used to compute the subjective value of an offer. Figure 1.4 illustrates the shape of each discounting function.

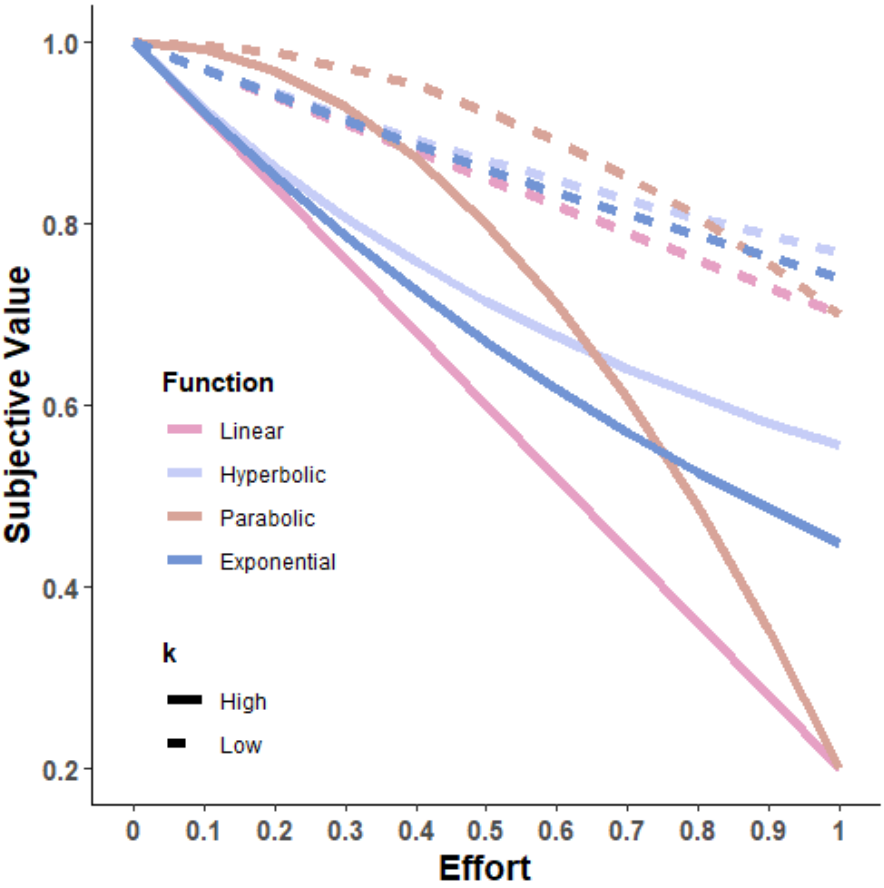

Figure 1.4: Discounting Functions. Subjective value of a 1-unit reward decreases monotonically as a function of increasing effort demand. The magnitude of the discounting k parameter regulates the degree to which a reward is devalued by effort demands. Lower discounting factors result in less subjective devaluation of reward as a function of increasing effort, while larger discounting factors result in steeper devaluation of reward as a function of increasing effort. In this case, low k parameter was set to .3 and high k parameter was set to .8.

Several studies relate brain activity locked to effort/reward cue or choice presentation to these subject- and trial-specific subjective value estimates. Subject-specific subjective value estimates can also be inputted back into the *softmax* function to estimate the probability that a given subject will accept one effortful reward option over another. Correlations between brain activity and this probability of choice metric are also often investigated. These distinctions will be relevant for the next section, which will review the neural underpinnings of net value for effort-based rewards.

1.3.2 Neural Correlates of Net Value and Effort-Based Reward

Over the past two decades, extensive research in both animals and humans has demonstrated that the key regions engaged in reward processing are also sensitive to cost valuation. Animal studies suggest that net value of rewards are encoded in a core valuation system composed of the VTA, NAcc, and basolateral amygdala, and that these regions are engaged in choices about rewards with effort, delay, and probability costs alike (Bailey et al., 2016). Critically, DA manipulations in these regions alter effort-based decision-making and motivated behavior in rodents. Furthermore, the role of mesolimbic DA in effort-based decision-making appears to be bi-directional, such that interference with DA transmission biases preferences to the low-effort option, while augmenting DA transmission increases selection of high-effort options in both T-maze and progressive ratio tasks (Salamone et al., 2018). These findings have been replicated using a variety of methods to alter DA transmission, such as administration of DA antagonists and agonists, depletions of local DA using neurotoxin injections, lesions of midbrain DA structures, and optogenetics (Floresco et al., 2008; Hauber and Sommer, 2009; Mai et al., 2012; Salamone et al., 2007; Salamone et al., 2018; Winstanley and Floresco, 2016). Of key interest is the VS, and more specifically the nucleus accumbens (NAcc), which has been shown to regulate movement- and value-related signals associated with effort-based rewards. These signals may arise from distinct neural populations within the striatum, such that the NAcc core and shell help regulate computations related to effort-based choice, whereas the NAcc core is more directly responsible for the invigoration and persistence of motivated behavior (Bailey et al., 2016). In humans, the VS also plays a critical role in tracking the net value of cost-based rewards. Specifically, fMRI studies have shown that the activity in the VS, along with the vmPFC, tracks delay- and probability-discounted subjective values (Dreher, 2013; Haber and Knutson, 2010; Knutson et al., 2005; D. J. Levy and Glimcher, 2012; I. Levy et al., 2010; Peters and Büchel, 2009; Prévost et al., 2010). Meta-analytic results indicate that the vmPFC and VS consistently scale positively with subjective value of rewards during decision-making (Bartra et al., 2013; D. J. Levy and Glimcher, 2012), making them candidate hubs for processing net value.

However, several experiments have failed to find a relationship between activity in this general valuation network and the net value of effort-based rewards (Chong et al., 2017; Croxson et al., 2009; Klein-Flugge et al., 2016; Kurniawan et al., 2010; Massar et al., 2015; Prévost et al., 2010; Schmidt et al., 2012; Suzuki et al., 2021), thus calling into question the existence of a unitary corticostriatal system for net value representation. Instead, a large body of evidence supports the hypothesis that specific neural substrates are recruited based on the specific cost feature being weighed. For instance, in rodents, risky rewards engage the medial OFC while delayed rewards engage the lateral OFC and prelimbic and infralimbic medial PFC (Bailey et al., 2016). Critically, the ACC appears to be a critical node for representing the value of effortful reward (Bailey et al., 2016). For example, lesions to the rodent homolog of the dACC and to the primate dACC have been shown to induce a shift in preference away from larger and more effortful rewards in favor of smaller and less effortful rewards (Rudebeck, Buckley, et al., 2006; Walton et al., 2003; Walton et al., 2007; Walton and Mars, 2007, but see Walton et al., 2005). Critically, when effort costs are equalized, rodents return to choosing the larger reward, suggesting that the ACC is nonessential when decisions can be resolved relying purely on reward value (Floresco and Ghods-Sharifi, 2007; Rudebeck, Walton, et al., 2006; Walton et al., 2003). Data from single neuron recordings also suggest that the ACC is one of the only prefrontal structures that consistently tracks effort costs throughout the course of decision-making (Kennerley et al., 2011; Kennerley and Wallis, 2009; Kennerley et al., 2006; Wallis and Kennerley, 2011), making it a candidate substrate for facilitating the integration of effort costs and reward values throughout the time course of reward processing.

A similar regional specialization based on cost features has also been proposed for humans. Specifically, the ACC, insula, midcingulate, and supplementary motor area (SMA) are significantly more activated in representing effort-discounted compared to time-discounted (Massar et al., 2015; Prévost et al., 2010) and probability-discounted subjective values (Burke et al., 2013). Furthermore, the ACC has been shown to encode both effort costs and integrated cost/benefit values, with blood oxygenation level dependent (BOLD) activity generally scaling positively with increasing effort demands and negatively with the subjective value of decision options (Chong et al., 2017; Klein-Flugge et al., 2016; Prévost et al., 2010). Intriguingly, activity related to SV encoding during effort-based decision-making is found only partially and, oftentimes, exclusively outside of the core valuation network. For example, Bonnelle et al. (2016) found that cost/benefit weighting of two effortful reward options positively correlated with BOLD activity in the ACC and pre-SMA, but negatively correlated with activation in the vmPFC. Seaman et al. (2018) also found that BOLD activity in the VS and ACC/mPFC was associated with the subjective value of the selected option in an effort-based decision-making task. However, in several studies, a relationship between activity in the VS/vmPFC and subjective value encoding is completely absent. For example, the ACC, pre-central gyrus and insula, but not the VS and vmPFC, were shown to track the SV of effortful choice and effort demand in a physical and cognitive task (Massar et al., 2015; Prévost et al., 2010). Klein-Flugge et al. (2015) also showed that the difference in subjective value between two effortful options was encoded by BOLD activity in the dACC and SMA, but not the common valuation network, and that activity in these substrates scales with both reward difference and effort difference. Finally, a study by Chong et al. (2017) identified a network composed of the dACC/dmPFC, dlPFC, the intraparietal sulcus, and the anterior insula as being involved signaling the subjective value of a reward across both cognitive and physical effort demands. Further, activity within these domain-general areas also covaried negatively with reward and positively with effort, suggesting an integration of these parameters within these areas (Chong et al., 2017). Critically, even in a region-of-interest analysis activity in neither the VS or vmPFC were shown to relate to subjective value encoding, suggesting a limited role for the common valuation network in encoding effort-based reward value (Chong et al., 2017) . These conflicting findings necessitate further exploration into the factors driving these divergent signaling patterns of effort-based reward representation.

1.3.3 The Peculiar Case of Effort

How is it that sometimes effort-based rewards are represented like other cost-based rewards while other times effort-based rewards are treated as something unique? One potential explanation for the lack of convergence in previous findings could be that differences in previous methodologies and uncontrolled confounds are driving these results. We will now review some of the methodological differences that could contribute to these divergent findings, as well as some of the relevant confounds that arise when designing effort-based reward paradigms.

1.3.3.1 Caveats of Measuring Effort-Based Reward

Domains of Effort. As reviewed earlier, there are several paradigms used to measure cost-based decision-making. Probability and delay discounting use costs with unitary measures that rely on an objective scale. That is to say that while the magnitude can change (i.e. 10% vs 90% chance or 1 day vs. 100 days), the cost itself is grounded in an objective unit of measure. In the case of effort however, several different methods have been used to manipulate demand and it remains unclear whether all effort is processed in a common, domain-independent manner. One central line of research has been to determine if cognitive and physical effort costs are represented in separate or overlapping regions in the brain. In rodents, inactivation of the ACC increases willingness to expend cognitive effort for a food reward (Hosking, Lam, et al., 2014), but decreases willingness to expend physical effort for food reward (Floresco and Ghods-Sharifi, 2007), suggesting dissociable effects within the same substrate. Behaviorally, individual differences in willingness to exert cognitive and physical effort are only moderately correlated within rodents at baseline (Cocker et al., 2012; Hosking, Cocker, et al., 2014; Hosking et al., 2015). In humans, individual differences in cognitive effort discounting are only moderately positively related to individual differences in physical effort discounting under conditions of hypothetical (Ostaszewski et al., 2013) and real (Lopez-Gamundi and Wardle, 2018) effort costs. In another adult sample, choices about cognitive effort were best modelled with a hyperbolic function while choices about physical effort were best modelled with a parabolic function, which suggests that the extent to which individuals devalue rewards and the mathematical nature of that discounting effect depends on the domain of the effort itself (Chong et al., 2017). Imaging studies similarly suggest that effort-based rewards are processed in a domain-general network but also activate task-dedicated regions; however, the nature of this domain-general network remains a topic of active debate. For example, in a study using a mixed paradigm containing both an effortful cognitive task (the Stroop task) and a physical task (hand grip), VS activity significantly reflected performance level for both, while physical effort demands were primarily reflecting in the sensorimotor cortex and cognitive demands in the dlPFC and paracingulate cortex (Schmidt et al., 2012). However, in two effort-based decision-making tasks, cognitive and physical effort was subserved by a common network of areas, including the ACC/dmPFC, dlPFC, the intraparietal sulcus, and the anterior insula, with the right amygdala specifically tracking the subjective value of cognitive effort subjective value but no specific area tracking the subjective value of physical effort (Chong et al., 2017). Thus, one relevant open question is whether different domains of effort are processed in a similar manner and if there exists any consistently identifiable common neural basis in representing these different types of effort.

Certainty of Reward Delivery and Effort Execution. Another methodological feature that is unique to effort-based decision-making paradigms is the timing and uncertainty of effort execution and reward delivery. For example, in delay- and probability-discounting paradigms, costs are oftentimes not experienced and rewards are only delivered for a select few trials which are selected at the end of the task. This carries significant benefits, such as being able to use parametric measures with a wide range of reward, probability, and delay values and having many trials, allowing for more extensive modeling. However, one of the drawbacks is that rewards and their associated costs are generally hypothetical, thus it is difficult to conclude whether areas activated during probability- and delay-related choices in these paradigms are the same areas that are activated when making choices with real outcomes.

Many effort-based decision-making paradigms also use "hypothetical" rewards and effort. Specifically, many studies only require participants to execute the effort component (and therefore receive the corresponding reward) for a small, random selection of the choices made (Aridan et al., 2019; Bernacer, Martinez-Valbuena, Martinez, Pujol, Luis, Ramirez-Castillo, and Pastor, 2019; Chong et al., 2017; Chong et al., 2015; Hogan et al., 2019; Massar et al., 2015; Westbrook et al., 2019). Oftentimes, effort is only executed offline, such that no reward is received and no effort is executed during the task itself (Aridan et al., 2019; Arulpragasam et al., 2018; Chong et al., 2017; Hogan et al., 2019). This could create a significant confound as the VS and vmPFC have been found to be sensitive to real versus hypothetical reward in the context of effort (Scholl et al., 2017). Alternatively, due to the role of mesolimbic DA in action encoding (Syed et al., 2016), it is possible that subjective value is indeed signaled by the VS, but that this signal is muted by opponent behavioral activation signals that arise in effort-based decision-making paradigms. For example, a study by Suzuki et al. (2021) found that activity in the VS was increased when anticipating and initiating effort in a non-choice (passive) effort-based reward task where effort was performed online. Conversely, the authors also found that VS BOLD responses were significantly lower for delivery of a reward that had required more, as opposed to less, effort, consistent with a discounting signal (Suzuki et al., 2021). However, in the same study, activity in the VS did not correlate with subjective value of the chosen option in a separate effort-based decision-making task where effort was performed offline. In a cross-paradigm analysis, Suzuki and colleagues (2021) found that VS responses to effort initiation in the online effort task were significantly positively associated with VS responses to prospective effort cues during the decision-making task, suggesting that there is an effort activation signal present in the VS even when effort demands will not be immediately executed. Similarly, that VS responses to discounted value during reward delivery in the online effort task were numerically negatively associated with VS responses to prospective effort cues during the decision-making task, providing trending support for a negative effort-discounting signal in the VS (Suzuki et al., 2021). Thus, the existence of opposing effort-activation and effort-discounting signals in the VS could explain why some studies fail to find net value encoding in the striatum (Arulpragasam et al., 2018; Chong et al., 2017; Hogan et al., 2019; Massar et al., 2015), but cannot explain why the VS is activated in other experiments where effort is executed online and effort-activation signals would be presumably more salient (Bonnelle et al., 2016; Hauser et al., 2017; Klein-Flugge et al., 2016).

Differences in Reward Rate. In paradigms with online effort exertion, it is relatively common to find lower success rates in the high demand condition (Aridan et al., 2019; Gaillard et al., 2019; Grodin et al., 2016; Ma et al., 2014; "Neural Correlates of Successful and Unsuccessful Strategical Mechanisms Involved in Uncertain Decision-Making", 2015; Schevernels et al., 2014; Umemoto et al., 2022; Westbrook et al., 2019; Yi et al., 2020. In some studies, the difference in success rates is small (<3%) and potentially imperceptible (Botvinick et al., 2009; Stoppel et al., 2011; Vassena, Silvetti, et al., 2014), while in other studies, differences in success rates are large and task difficulty (i.e. effort demand) is directly manipulated by lowering the probability of success (Ma et al., 2014; Silvetti et al., 2014). These differences in success rates result in less cumulative reward under high effort conditions, thereby confounding effort demands with reward rate. This is critical, as some of the effects observed in effort-based reward preference may be driven by estimates of reward likelihood instead of effort cost. For example, it has been observed that participants also modulate behavior on the basis of average reward rate rather than instantaneously available reward (Guitart-Masip et al., 2011). Increased reward rates have also been shown to invigorate behavioral responses; this relationship is also mediated by midbrain dopamine (Beierholm et al., 2013). Furthermore, midbrain DA and the common valuation network modulate probability discounting behavior (Bailey et al., 2016) and encode probability during reward anticipation (Bretzke et al., 2021; Yacubian et al., 2007), opening the possibility that striatal activity during effort-based decision-making could reflect a probability signal as well. Activity in the anterior insula and mPFC/ACC have been shown to track both probability and effort discounted subjective value (Burke et al., 2013; Seaman et al., 2018), suggesting that there is also a partial overlap in regions associated with signaling the subjective value of these two costs even outside of the common valuation network. Finally, reward rate has been repeatedly shown to modulate outcome processing. For example, increased reward rate potentiates the learning of action-outcome associations, a process heavily mediated by striatal DA (Taswell et al., 2018). Component P300, as well as EEG signals originating from the mPFC (FRN and frontal midline theta) have all been shown to be sensitive to reward probability and expectation at outcome (Bellebaum et al., 2010; Cavanagh et al., 2012; Hajcak et al., 2007; Hajihosseini and Holroyd, 2013; Oliveira et al., 2007; Rawls et al., 2020; Silvetti et al., 2014; Wu and Zhou, 2009). Therefore, one critical consideration when designing effort-based decision-making paradigms is to either experimentally or statistically control for demand-driven differences in reward rates.

Metrics of Subjective Value. Another important observation about the different effort-based reward paradigms is whether subjective value is measured using a choice metric or by simple main and interaction effects of effort. Current evidence partially supports the role of the common valuation network and the ACC in signaling prospective net value of effort-based rewards in the absence of choice. Activity in the VS has been shown to track prospective incentive value for rewards with effort requirements (Gaillard et al., 2019; Schmidt et al., 2012). In Croxson et al. (2009), BOLD activity in both the VS and ACC scaled with the net value of prospective effort-based rewards. Another study also found that the ACC and striatum were sensitive to both prospective cognitive effort and reward anticipation (Vassena, Silvetti, et al., 2014). Krebs et al., (Krebs et al., 2012) found enhanced BOLD responses in the vmPFC and dorsal striatum for both anticipated effort and reward, but that responses in the VS and pre-SMA were predominantly sensitive to prospective reward and effort, respectively. In contrast, the ACC and pre-SMA have also been shown to weakly predict upcoming effort expenditure and instead predominately signal upcoming reward incentives, while the activity in the vmPFC and VS more consistently related to prospective reward, effort, and average effort exertion (Kroemer et al., 2014). Further, Stoppel et al. (2011) found that activity in the VS and midbrain/SN tracked reward magnitude and difficulty at cue but that activity in the ACC was sensitive to reward and effort only immediately prior to effort execution (target period) and at feedback. This finding converges with a recent coordinate-based meta-analysis which shows that the ACC was not consistently engaged in cue valuation signaling of upcoming rewards and cognitive control demands but was consistently engaged during the target period (Parro et al., 2018). Taken together, these findings implicate the common valuation system in encoding the net value of effortful rewards in the absence of choice, although it remains unclear why only select regions of this network are recruited in some studies while others engage both the VS and vmPFC. Furthermore, the conditions under which the ACC is recruited for net value signaling also remain unclear.

One proposal is that the ACC is recruited for to execute the cognitive functions that subserve option comparison and decision-making (Kennerley et al., 2006; Kolling et al., 2016; Shenhav et al., 2014). If this were the case, one would expect that the ACC would be more consistently engaged in effort-based decision-making tasks. Specifically, activity in the ACC, along with a series of other regions associated with cognitive control (i.e. dlPFC, insula, intraparietal sulcus (IPS)), has been shown to scale negatively with subjective value and the magnitude of difference between subjective values of the two options on offer. For example, in a physical effort-based decision-making task, similarity in net value between options (i.e. “cost-benefit weighing load”) positively correlated with BOLD activity in the dACC and pre-SMA, but negatively correlated with activation in the vmPFC (Bonnelle et al., 2016). In a similar handgrip task, activity in the dACC and SMA, but not the vmPFC or VS, encoded the difference in subjective value between effortful reward options (SV difference), and scaled negatively with reward difference and positively with effort difference (Klein-Flugge et al., 2016). BOLD activity in the ACC-insula network scaled negatively with the subjective value of the variable effortful option in physical effort-based reward task (Prévost et al., 2010). In this case, since the alternative offer had a fixed effort and reward, this metric of subjective value was analogous to SV difference. However, BOLD activity in the mPFC/ACC and VS has also been shown to scale positively with subjective value of chosen option in a key-press effort-based decision-making task (Seaman et al., 2018), highlighting the importance of the subjective value metric used when interpreting the direction of neural activity. Activity in the dACC/dmPFC, dlPFC, IPS, and the anterior insula has been shown to scale negatively with SV difference in both a cognitive and physical effort-based decision-making task (Chong et al., 2016). Interestingly, Massar et al. (**2015**) found that the subjective value of the variable effortful option correlated with activity in the left temporal and bilateral parietal cortices, as well as the dlPFC, but that subjective value of the chosen option correlated with activity in the ACC, again highlighting the sensitivity of some subjective value metrics in capturing specific valuation signals even within the same paradigm.

One common observation is that the SV difference metric approximates decision difficulty. Thus, one plausible interpretation is that regions that are more typically associated with cognitive control itself, such as the ACC, IPS, dlPC, and insula, are recruited to support the cognitive control functions that subserve decision-making. This proposal would explain why these regions are active when SV difference is small and why signals in these regions generally become weaker when the subjective value of a single option is large (i.e. presumably when SV difference is large, at least in effort-based decision-making paradigms). In fact, the two studies that experimentally controlled for decision difficulty found that BOLD activity in the ACC encoded for decision difficulty while activity in the VS and vmPFC tracked the subjective value of effort-based reward. In a novel experiment by Westbrook et al. (2019), participants first completed an effort discounting task to generate an estimate of their individual indifference points. Later these custom indifference points were used to set the value of the rewards-on-offer in a cognitive effort-based decision-making task. This allowed experimenters to create a custom measure for decision difficulty, since choices where offers were close to the indifference point were considered difficult, while offers that were far from the indifference point were considered easy. They found that the cognitive control network, comprised of the dACC, dlPFC, and IPS, but not the common valuation network, were more active on difficult versus easy decision trials; conversely, activity in the VS and vmPFC not only correlated with single-offer SV, but also scaled positively with reward amount and negatively with effort demand (Westbrook et al., 2019). In a similar vein, Hogan et al. (2019) used a non-rewarded effort-based decision-making task to disentangle the effects of choice difficulty from subjective effort valuation. Interestingly, Hogan and colleagues (2019) found that the vmPFC tracked the subjective value of effort as well as the difference in effort values, but that the ACC scaled with choice difficulty (as measured by reaction time). Taken together, these findings suggest that the common valuation network subserves subjective valuation of effortful rewards and option comparison, but that the ACC is recruited when decisions are more difficult and require more cognitive control, such as when options are very similar in value.

This interpretation of the ACC aligns well with neurocomputational frameworks which propose that the ACC is involved in motivated control, or the promotion of successful selection and invigoration of behavioral response in goal-directed behavior (Shenhav et al., 2013; Vassena, Deraeve, et al., 2017). Specifically, the Expected Value of Control (EVC) theory posits that the dACC integrates a variety of signals – including reward, cost, uncertainly, as well as other state variables and control-relevant information – to determine the degree of control worth allocating to a task (Shenhav et al., 2013). Each control signal has an identity (e.g., which task to perform, which cognitive mechanism to employ, which choice to select) and an intensity (e.g., how much control to employ); the ACC is responsible for selecting the control signal that maximizes the EVC. This model has successfully linked neural activity and behavioral correlates to performance efficacy (Frömer et al., 2021; Grahek et al., 2022) and attention allocation (Shenhav et al., 2018). In the case of choice difficulty, the EVC account predicts increased dACC involvement as offers become increasingly similar in value (Shenhav et al., 2013; Shenhav et al., 2021). However, the EVC model would also predict that optimal control signals would decrease when choices become too similar in expected value, as added control is not necessary since both options are equally valuable (Vassena et al., 2020). Although one study has directly tested this hypothesis (Vassena et al., 2020), other experiments are needed to examine this activation patter for choices about effortful reward. This computational framework also proposes that the dACC monitors outcome-value information in order to estimate EVC (Shenhav et al., 2013). This claim is supported by the dACC's involvement in conflict monitoring (Botvinick and Braver, 2015; Botvinick et al., 2001; Laird et al., 2005), responsivity to positive and negative outcomes (Bartra et al., 2013; Holroyd and Coles, 2002; Kouneiher et al., 2009), and relationship with prediction errors (Amiez et al., 2012; Kennerley et al., 2011). To fully test these hypotheses however, future research will need to measure dACC activity in response to effortful rewards both at the time of decision and at outcome.

1.3.3.2 Contradictory Effects of Effort

Of key interest then is to understand how effortful rewards are valued at the time of receipt. While virtually all research focusing on the cue evaluation or decision-making period assumes that prospective effort attenuates the value of a future reward, a growing body of work suggests that expended effort actually potentiates the value of a reward. So while people are generally effort avoidant and will only engage in effort when the incentives are large enough, it is also true that rewards gained under more effort are deemed more valuable (Inzlicht et al., 2018). This observation has been deemed the "effort paradox", as it completely contradicts the effort discounting perspective that predominates the neuroeconomic framework.

This psychological phenomenon has been observed in a variety of contexts and several frameworks have been used to reconcile these two contradictory effects of effort. For example, studies of consumer behavior observed that people value furniture more when they assembled it personally as compared to when assembled by a professional, an observation known as the IKEA effect (Norton et al., 2012). Alternatively, justifications of effort were also explained by cognitive dissonance theory, which proposes that effort is indeed aversive, but that individuals change their attitudes about a reward to justify past effort (Covey, 2009). However, in some cases it appears that effort itself is deemed rewarding. For example, many animal species prefer to work for food even when they can obtain an identical amount of food without effort, a behavior referred to as contra-freeloading (Inglis et al., 1997). Significant research has also been done on the personality trait "need for cognition", which refers to a person's tendency to engage in and enjoy cognitively effortful tasks (Cacioppo et al., 1996). Independent of whether or not effort itself is valued, the idea that working for a reward increases the value attributed to that reward appears relatively universal.

Evidence of effort's added value has also been demonstrated by activity in the common reward valuation system and EEG markers related to reward processing. Specifically, BOLD activity in the VS and the subgenual ACC has been shown to be higher for rewards gained under high compared to low effort (Gaillard et al., 2019). Both the ventral and dorsal striatum had stronger responses to rewards that required instrumental responses compared to reward that did not (Zink et al., 2004). This converges with evidence that the P300 amplitudes are larger for rewards that subjects obtained by performing an action as opposed to inhibiting a response (Schevernels et al., 2016). Component P300 has also been shown to be enhanced in response to reward after exerting high, but not low, effort (Ma et al., 2014). Furthermore, positive performance feedback on difficult compared to easy arithmetic tasks also elicited an enhanced P300, suggesting that effort itself can increase saliency (Ma et al., 2014; Wang et al., 2017). Execution of high-effort compared to low-effort also resulted in increased amplitudes in an EEG signal related to reward processing in the ACC (Reward Positivity; RewP), consistent with increased valuation of reward outcomes by ACC (Umemoto et al., 2022).

However, other studies suggest that effort has a limited or even discounting effect at feedback.

For example, activity in the VS and vmPFC scaled positively with reward magnitude at feedback, this effect was not modulated by physical effort demand (Prévost et al., 2010). NAcc activation to reward delivery was blunted after completing more demanding, as opposed to less demanding, working memory (2014 and cognitive effort tasks (2009). In fact in Botvinick et al. (2009), high effort expenditure resulted in a deactivation in the NAcc for no reward outcomes, consistent with the idea that effort is costly and devalues reward (Botvinick et al., 2009). Anterior VS BOLD responses to reward have been shown to be attenuated after exerting higher degree of effort in a navigation task (Suzuki et al., 2021). P300 amplitudes have also been shown to be enhanced for rewards received after low, compared to high, effort expenditure, again consistent with an effort discounting effect (Bowyer et al., 2021).

One effective strategy for understanding how both prospective and expended effort demands impact the subjective valuation of reward would be to measure the impact of effort during both reward anticipation and reward delivery. For practical reasons (e.g., offline effort execution, reduced task length, etc.), most studies only analyze data locked to the initial evaluation phase or to effort execution and feedback. Of the effort-based reward studies that measure brain activity at both cue valuation/choice and feedback phases, only a handful utilized fMRI (Gaillard et al., 2019; Prévost et al., 2010; Schmidt et al., 2012; Stoppel et al., 2011; Suzuki et al., 2021). Furthermore, despite the high temporal resolution of EEG imaging, relatively few studies have looked at the EEG signals related to effort-based reward processing starting at the cue evaluation or decision-making period (Schevernels et al., 2016; Schevernels et al., 2014; Silvetti et al., 2014; Umemoto et al., 2022). Significant methodological differences between fMRI and EEG effort-based reward tasks make it difficult to consolidate results and draw conclusions. Additionally, virtually all of the studies that used EEG to study net value of effort-based rewards have focused on one component (P300), ignoring more fine-grained aspects of how reward value and effort costs are signaled and integrated together during decision-making (but see Harris and Lim (Harris and Lim, 2016) for time course of separable effort, stimulus value, and net value signals in effortful choice). Components N2/FRN and oscillatory behavior in the theta frequency band would also be useful markers for ACC activity and could help elucidate the role of the ACC/mPFC in valuation of effort-based rewards at cue and outcome monitoring at feedback.

Another important strategy for studying the effect of effort on reward at feedback would be to remove confounding effect of reward likelihood. As discussed before, some paradigms have large differences in success rate – and therefore reward probability – between high and low effort conditions (Schevernels et al., 2014; Silvetti et al., 2014). This leaves open the possibility that effort-related neural responses during reward feedback are actually driven by the different reward probabilities under high and low effort. For example, feedback-P3 has been found to covary with both reward magnitude and probability (Yeung and Sanfey, 2004) and is sensitive to reward expectancy, so that it is generally enhanced for less probable compared to more probable gains (Hajcak et al., 2007; San Martín, 2012; Watts et al., 2017). FRN and RewP are also sensitive to reward probability and expectancy and are generally enhanced for reward prediction violations (Glazer et al., 2018; Sambrook and Goslin, 2015), such that these components could potentially be more enhanced under conditions where rewards were less likely under high effort. The VS and vmPFC have also been repeatedly implicated in signaling violation of reward expectancy at outcome, with findings from a fMRI meta-analysis concluding that this network is more consistently enhanced when reward outcomes are better-than-expected (Fouragnan et al., 2018). As discussed previously, since high effort rewards are generally more unlikely, it is plausible that enhancements in activity in the VS and vmPFC during delivery of high-effort rewards are a function of prediction violations as opposed to amplification of subjective value. Controlling for the difference in reward rates between effort demands is therefore critical for identifying a pure effort signal at feedback.

1.3.3.3 Effort as a Reinforcer

As suggested in the previous section, several of the neural substrates and markers involved in effort-based reward processing at feedback are also implicated in reward learning. More specifically, the ventral striatum has been repeatedly shown to encode reward prediction error in both animals and humans (Abler et al., 2006; Cohen, 2007; Daniel and Pollmann, 2014; Jocham et al., 2011). Meanwhile, the vmPFC has also been shown to track the learned subjective value of an option independent of the sensorimotor demands of the task (Jocham et al., 2011; Vassena, Krebs, et al., 2014), which falls in line with accounts of the vmPFC as a central node for signaling abstract reward values once these values have been computed elsewhere (Padoa-Schioppa, 2011). Single unit recordings (Kennerley et al., 2011), EEG signals (Cavanagh et al., 2012; Chase et al., 2011; Mas-Herrero and Marco-Pallarés, 2014; Oliveira et al., 2007; Silvetti et al., 2014; Talmi et al., 2013), and BOLD activity (Vassena, Krebs, et al., 2014) all indicate that activity in the ACC/mPFC tracks the discrepancy between expected and actual rewards. Several have also proposed that the size of the FRN, an EEG component thought to be generated in the ACC, is predictive of reward learning (see Luft (2014) for a comprehensive review). Another putative marker of ACC function – frontal midline theta – has also been shown to correlate with prediction errors and individual differences in reward learning (Mas-Herrero and Marco-Pallarés, 2014). In all, these findings suggest that the VS and ACC – two regions that play a very important role in net value signaling – are also highly involved in signaling violations of expected reward during feedback.

Effort-based reward processing, however, requires more than simple reward prediction. Unlike traditional classical conditioning, where feedback is only informative about the stimulus-reward association, feedback during effort-based reward processing reveals relevant information about the value of the action and performance. This complicates the interpretation of feedback-related brain activity in effort-based reward paradigms since net valuation occurs in overlapping temporal windows and neural substrates as action-value updating and performance monitoring. For example, the striatum has been shown to update the value of a chosen action based on the outcome (Ito and Doya, 2009; Kim et al., 2009). In humans, the VS signals violations in reward expectation, with greater physical effort attenuating this signal (Kurniawan et al., 2013). While the VS appears to incorporate some aspects of effort value with reward prediction, it remains unclear to what degree the ACC integrates the two. For instance, BOLD activity in the ACC/mPFC and anterior insula have been shown to reflect the discrepancy between expected and actual efforts, but not between expected and actual reward (Hauser et al., 2017; Skvortsova et al., 2014). However, effort has been shown to modulate subjective value prediction error signals in BOLD activity in the ACC at cue (Arulpragasam et al., 2018), which implies that the ACC weighs effort costs in violations of expected subjective value. Neurons in the ACC have also been shown to integrate motor information with outcome predictions (Cowen et al., 2012; Hyman et al., 2017), update action values (Mashhoori et al., 2018), track trial-by-trial information (Akam et al., 2021; Kawai et al., 2015) and correlate with behavioral adjustments (Akam et al., 2021). The role of the ACC in adapting behavior on the basis of performance monitoring and reward prediction has led to proposals that the dACC serves as a reinforcement learning agent that optimizes adaptive resource allocation via cortico-brainstem recursive loop (Silvetti et al., 2018). According to the Reinforcement Meta-Learner theory, the dACC tunes reward and prediction signals (broadcasted by VTA-DA) and learning signals about the environment (broadcasted by noradrenergic release from locus coeruleus) for the purpose of selecting optimal behavioral responses (Silvetti et al., 2018). This new theoretical perspective highlights the importance of elucidating how effort demands impact learning signals and the consequences this has for effort-based choice.

In the preceding sections, we provided an overview of the fundamental theoretical and neural foundations pertaining to the evaluation of rewards and effort. We emphasized existing knowledge regarding the localization and integration of costs and benefits within the brain. However, this concise analysis also underscored several apparent contradictions in the literature. Notably, signals related to rewards with effort requirements are frequently absent in the common valuation system, indicating the involvement of a distinct yet partially overlapping set of brain regions involved in the integration of effort costs and reward value. The diversity of experimental designs used to assess effort-based reward processing, as well as the potential confounds generated by these paradigms, pose challenges in interpreting findings and may account for some of these disparate results. Additionally, another contradictory observation is that individuals often exhibit a preference for prospective rewards requiring less effort, while concurrently assigning higher value to rewards attained through greater effort. This indicates the presence of a dissociation that necessitates further investigation into the integration of effort costs with value across various stages of reward processing.

Chapter 2

Research Aims

The overarching objective of the current work was to investigate the influence of effort costs on the processes involved in evaluating rewards. Specifically, our aim was to determine where in the brain the subjective value of effort-based rewards is represented and how effort costs impact these representations across the different phases of reward processing. To achieve this primary goal, we divided our investigation into three main research questions.

First, we aimed to identify brain regions that consistently (and across experimental paradigms) signal prospective effort costs and net value of effort-based rewards. Building on previous literature, we anticipated that prospective effort demands would be signaled in frontal regions such as the ACC, SMA, and AI. However, conflicting findings regarding the neural correlates of net value prompted us to explore whether these signals are consistently observed in the core valuation network (including the orbital and ventromedial prefrontal cortex and the striatum) or in more frontal regions.

Second, we aimed to examine to what extent the mPFC (which includes the pre-SMA and ACC) selectively tracks pure effort costs and net value signals in the absence of several confounds, and the extent to which this signal varies over the course of reward processing. We hypothesized that the mPFC – putatively measured by frontal midline theta activity – would track the net value of prospective effort-based rewards and that effort would enhance reward-related signals during feedback. However, the precise nature of this net value signal and whether it follows a discounting pattern or resembles the need for control, remained an open question.

Third, we sought to determine if the net value of effort-based rewards could be tracked through the learning of stimulus-outcome associations. Specifically, we hypothesized that the subjective value of effort-based rewards would modulate the learning of cue-reward associations. We presented two opposing predictions: if effort discounts the value of the reward, we expected that contingencies of rewards requiring higher effort would be learned more rapidly compared to those requiring lower effort. Conversely, if effort enhances the saliency of reward feedback, we anticipated that rewards with higher effort requirements would be learned more quickly than those with lower effort requirements. The three following studies were implemented to achieve these aims.

2.1 Study 1: Identifying areas consistently involved in effort valuation and net value signaling

As discussed above, previous studies implicate a general valuation system comprised of the VS and vmPFC in encoding the net value of prospective rewards. However, several reports suggest that the subjective value of effort-based rewards is not processed in this general valuation system, but rather in the ACC, pre-sensory motor area (pre-SMA), and anterior insula, brain regions which are associated with cognitive control (Kouneiher et al., 2009; Parro et al., 2018). Further, the diversity of paradigms and neuroeconomic measures used in effort-based decision-making studies make it difficult to parse apart whether these regions are signaling the prospective demands and integrated net values of effort-based rewards, or simply engaged in cognitive control processes that subserve the decision-making features of these experimental paradigms. One way to identify which brain regions are systematically recruited for effort valuation and cost-benefit integration is to look for overlapping activity across a variety of effort-based reward paradigms. To this aim, we designed and executed a hybrid coordinate- and image-based fMRI meta-analysis of effort-based reward studies. The methods and findings of this study are reported in Chapter 3.

2.2 Study 2: Isolating the effect of effort demands, reward magnitude, and reward probability in mPFC effort-based reward processing

The majority of studies investigating effort-based reward have relied on paradigms that either 1) limit analyses to one phase (anticipation vs feedback) of reward processing, 2) do not require participants to reliably execute effort demands to receive the reward and 3) have lower reward rates for high effort options. The third observation in particular presents a crucial confound in effort-based reward studies, as rewards might be devalued based on lower reward probability as opposed to increased effort demands.

To disentangle the effects of reward probability from signals of effort-based reward, we developed a novel paradigm which equalized success rates (and therefore reward rates) between levels of effort demand. We then used scalp electroencephalography (EEG) techniques to investigate how frontal midline theta (FMT) – an oscillatory index of cognitive control and a putative measure of mPFC functioning – and the event related component P300 – an EEG marker of incentive salience – responded to prospective and experienced rewards with varying effort demand requirements and reward probabilities (Cavanagh and Frank, 2014; Glazer et al., 2018; Mas-Herrero and Marco-Pallarés, 2016). This study can be found in Chapter 4.

2.3 Study 3: Identifying the effects of cognitive effort expenditure on reward prediction and learning

Many of the brain regions involved in reward prediction and behavioral adaptation to reward (e.g., VS and ACC) have also been implicated in tracking the net value of effort-based rewards.

Furthermore, since the strength of reward prediction errors (RPEs) and learning of stimulus-outcome contingencies depends on the quantity, quality, and subjective value of a reward (Lak et al., 2014; Roesch et al., 2007; Schultz et al., 2015; Stauffer et al., 2014), it would follow that effort-requirements could impact the value of the reward and therefore the learning of these contingencies. Thus, reward learning paradigms could provide a perfect proxy for exploring the effect of effort expenditure on net value estimates of reward. In fact, a recent study in non-human primates, found that dopamine neurons in the VTA increased firing in response to cues predicting reward and to reward delivery after exerting more, compared to less, effort (S. Tanaka et al., 2019). These neurophysiological responses were coupled with behavioral effects, such that subjects learned stimulus-reward associations more quickly when exerting more, compared to less, effort for a reward (S. Tanaka et al., 2019). However, to date, the impact of effort on reward learning has not been investigated in humans.

To this aim, we modified a common reward learning paradigm (the Reversal Learning Task), where stimulus-reward contingencies were learned through experience and participants were required to perform either a high or low cognitively demanding task in to obtain the reward. We then fit choice data using a reinforcement model to formally test the hypothesis that learning rates are modulated by the net value of rewards with high vs. low effort costs. Our hypothesis was two-fold. If effort costs devalued the benefits of reward, participants should acquire stimulus-reward associations more slowly for rewards that require higher effort costs. Conversely, if effort expenditure potentiates the value of subjective value of reward, participants should learn stimulus-reward contingencies more quickly for rewards that require higher effort costs. This experiment is discussed in Chapter 5.

Chapter 3

The neural basis of effort valuation: A meta-analysis of functional magnetic resonance imaging studies*

3.1 Abstract

Choosing how much effort to expend is critical for everyday decisions. While several neuroimaging studies have examined effort-based decision-making, results have been highly heterogeneous, leaving unclear which brain regions process effort-related costs and integrate them with rewards. We conducted two meta-analyses of functional magnetic resonance imaging data to examine consistent neural correlates of effort demands (23 studies, 15 maps, 549 participants) and net value (15 studies, 11 maps, 428 participants). The pre-supplementary motor area (pre-SMA) scaled positively with pure effort demand, whereas the ventromedial prefrontal cortex (vmPFC) showed the opposite effect. Moreover, regions that have been previously implicated in value integration in other cost domains, such as the vmPFC and ventral striatum, were consistently involved in signaling net value. The opposite response patterns of the pre-SMA and vmPFC imply that they are differentially involved in the representation of effort costs and value integration. These findings provide conclusive evidence that the vmPFC is a central node for net value computation and reveal potential brain targets to treat motivation-related disorders.

3.2 Introduction

Every day, we are faced with choices about whether to invest effort to attain certain goals (Bailey et al., 2016; Salamone et al., 2009). These effort demands are often regarded as costly, such that individuals tend to avoid one action if it requires too much effort with respect to the reward it entails (Kool et al., 2010; Kurniawan et al., 2010; Kurniawan et al., 2011; Lopez-Gamundi and Wardle, 2018; Salamone et al., 2018). The ability to accurately weigh energy requirements against potential benefits (e.g., "effort-based decision-making"), is therefore crucial for optimal goal-directed action, and alterations in this function are believed to be a core component of

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*This study has been published in Lopez-Gamundi, P., Yao, Y-W, Chong, T. T-J., Heekeren, H. R., Mas-Herrero, E. & Marco-Pallarés, J. (2021). The neural basis of effort valuation: A meta-analysis of functional magnetic resonance imaging studies. Neuroscience & Biobehavioral Reviews, 131. Text, tables and figures are a reproduction of the article.

motivational disorders, such as apathy (Chong and Husain, 2016; Hartmann et al., 2015; Husain and Roiser, 2018), and have been found across a variety of psychopathologies, including depression (hua Yang et al., 2014; M. T. Treadway, Bossaller, et al., 2012), schizophrenia (Barch et al., 2014; Park et al., 2017), Parkinson's disease (Chong, 2018; den Brok et al., 2015; Le Heron et al., 2018), and substance dependence (Grodin et al., 2016). Due to its clear clinical importance, there has been a recent surge of interest in how effort devalues prospective rewards, and such studies have demonstrated that effort might be a unique cost, distinct from other more investigated cost domains, such as risk and delay. However, work on the neural mechanisms underlying effort-based valuation have yielded heterogeneous results, and the question of how humans integrate effort and reward remains a subject of contention.

Most behavioral economic theories of reward-related behavior rely on the assumption that an organism weighs a reward and its associated costs to generate a net value of an option (Kahneman and Tversky, 1979; Sutton and Barto, 1998; Von Neumann and Morgenstern, 1990). A popular hypothesis proposes that, to effectively compare different options, the net value of each must be represented in a 'common currency' (Padoa-Schioppa, 2011; Rangel et al., 2008; Westbrook and Braver, 2015). A network of regions, including the ventromedial prefrontal cortex (vmPFC; and adjacent orbitofrontal cortex) and ventral striatum (VS), have been repeatedly implicated in the encoding of the net value of rewards discounted by the costs associated with obtaining them (Bartra et al., 2013; D. J. Levy and Glimcher, 2012). Based on these data, this valuation network is posited to be 'domain-general', as it tracks net value representations regardless of the nature of the reward (e.g., primary vs secondary) (Bartra et al., 2013; Sescousse et al., 2013) or of the type of cost (e.g., risk vs delay) (Kable and Glimcher, 2007; Peters and Büchel, 2009; Prévost et al., 2010).

However, much of these data have focused on outcome-related costs such as risk or delay. Notably, research on effort-based valuation suggests a limited role for the vmPFC and VS for value integration. Instead, other frontal regions beyond this core valuation network, including the anterior cingulate cortex (ACC), supplementary motor area (SMA), and anterior insula (AI), have been shown to signal net value discounted by effort costs (Arulpragasam et al., 2018; Camille et al., 2011; Chong et al., 2017; Klein-Flugge et al., 2016; Massar et al., 2015; Skvortsova et al., 2014; Walton et al., 2003). These findings are consistent with animal studies showing that lesions to the ACC, but not the nucleus accumbens, prelimbic/infralimbic cortex (homologous to the vmPFC), or orbitofrontal cortex, reduce the amount of effort rats invested for rewards (Rudebeck, Buckley, et al., 2006; Walton et al., 2003; Walton et al., 2009). Furthermore, neural activity in the ACC, as measured by single unit recordings, varies with cost-benefit weighting (Hillman and Bilkey, 2010, 2012) and effort-related choice (Cowen et al., 2012). This body of work thus raises the possibility that a distinct frontal network is specifically recruited to integrate effort-related value.

On the other hand, these frontal regions (i.e. ACC, pre-SMA, AI, etc.) are also commonly implicated in cognitive control processes (Wu et al., 2020), which may overlap or obscure value signals. For example, value-based decision-making may trigger cognitive control functions such as conflict detection and response inhibition (Botvinick and Braver, 2015; Botvinick et al., 2001), surprise and/or prediction error signaling (Vassena, Deraeve, et al., 2017, 2020), and invigoration of goal-directed behavior (Kouneiher et al., 2009; Kurniawan et al., 2013; Mulert et al., 2005).Therefore, it is plausible that these regions are recruited to prepare and invigorate behaviors necessary for realizing a prospective reward instead of for computing prepotent net values per se. Cognitive control is also required for difficult decision-making, such as when two simultaneously presented options have similar net value (**Klein-Flugge206**; Chong et al., 2017; Hunt et al., 2012; Massar et al., 2015), and in exploration/exploitation and foraging contexts, where individuals forego more immediate, secure rewards in order to search for alternative reward sources (Kolling et al., 2016; Shenhav et al., 2013). Indeed, studies that have independently manipulated net value and decision difficulty showed that these frontal regions, particularly the dorsal ACC, specifically tracked decision difficulty (Hogan et al., 2019; Westbrook et al., 2019) while, in contrast, the vmPFC uniquely tracked net value (Westbrook et al., 2019). Similarly, exploration of the reward environment – a behavior which is associated with increased cognitive control since it requires forgoing the "default" reward option in favor of uncertain rewards – also engages the dACC (Amiez et al., 2012; Cavanagh et al., 2012 although see Daw et al., 2006 for overlap with vmPFC). Taken together, these findings suggest that this distinct frontal network is recruited more specifically for cognitive control, such as response planning, option comparison, and foraging, whereas effort-related value integration is still processed in the core valuation network (e.g., vmPFC and VS) that have been identified in other cost domains.

The inconsistencies in previous studies may be related to several issues. For example, some may have been statistically underpowered due to small sample sizes, which may have reduced the probability of detecting significant effects, and/or reduce the reliability of their findings (Müller et al., 2018; Poldrack et al., 2017). Furthermore, the specific effort requirements of each task may have induced different patterns of brain activity, making it difficult to judge whether findings from individual studies can be generalized to the cognitive process of interest. A promising approach to address these issues is to quantitatively synthesize fMRI data across multiple studies using an image-based meta-analysis (Müller et al., 2018). Relative to traditional meta-analyses based only on peak coordinates of significant activity, an image-based meta-analytic approach uses the full information of the statistical maps from each study, and has greater power to detect small effect sizes (Luijten et al., 2017; Salimi-Khorshidi et al., 2009). A previous study showed that even the inclusion of 20% of statistical maps for included studies could significantly improve the precision of a meta-analysis (Radua et al., 2012).

Here, we conducted a hybrid coordinate- and image-based fMRI meta-analysis to identify the neural correlates of effort-related cost processing and value integration. Considering their critical roles in response planning, we hypothesized that frontal regions like the ACC, SMA, and AI would be consistently involved in representing prospective effort, independent of the reward offer. We also aimed to test whether effort-related net value integration (i.e., the integration of reward value with the effort required to obtain it) relied on the core valuation areas such as the vmPFC and VS or broader frontal regions.

3.3 Materials and Methods

3.3.1 Literature Screen, Data Collection, and Preparation

3.3.1.1 Exhaustive Literature Search

We conducted a systematic literature search to identify neuroimaging studies on prospective effort and the integration of reward value and effort costs in healthy adults. Candidates for inclusion were initially identified by searching PubMed, ProQuest, and Web of Science on June 29, 2020 using the grouped terms (“fMRI” OR “functional magnetic resonance imaging”) AND (“effort discounting” OR “effort-based decision-making” OR “effort valuation” OR “effort anticipation” OR “cost-benefit valuation” OR “cognitive effort” OR “physical effort” OR “effort expenditure” OR “effort allocation” OR “effortful goal directed action” OR “reward related motivation” OR “reward related effort”). Searches were limited to human studies where databases would allow. 121, 787, and 127 studies were identified on PubMed, ProQuest, and Web of Science, respectively. We also searched existing in-house reference libraries and names of prominent authors in the field, resulting in the addition of candidate studies. 934 candidate studies remained after search results were pooled and duplicates removed. Two researchers (PL-G, Y-WY) then independently reviewed the title and abstract of candidate papers to determine relevance, resulting in a pool of 72 studies that underwent a full-text review (Figure 3.1).

3.3.1.2 Inclusion/Exclusion Criteria

Studies were included if they: 1) had a healthy adult human sample in the non-elderly age range (ages 18 to 65, with one exception detailed below); 2) used functional MRI; 3) either reported or referenced a whole-brain analysis; and 4) utilized a task with an effort component with clear effort (or combined effort and reward) cues during an ‘anticipation’ phase. Please note that ‘anticipation’ in this case refers to the evaluation of prospective effortful rewards before or during decision-making, and does not include anticipatory responses to reward post-effort exertion (e.g., the ‘evaluation’ phase described in Assadi et al., 2009).

To ensure that the selected studies could be meaningfully compared, we limited the final corpus to those that used experimental paradigms with certain characteristics. First, because studies have found that loss and gain are asymmetric and partially dissociable (Chen et al., 2020; Porat et al., 2014; S. C. Tanaka et al., 2014), we excluded studies that used paradigms with only loss conditions, or that only conducted gain vs loss comparisons. Second, we excluded studies that only used a single speeded response as its effort component (e.g. classical Monetary Incentive Delay task Knutson et al., 2000), as this was not deemed as a significant effort demand, and other reviews and meta-analyses focusing on reward anticipation with these paradigms can be found elsewhere (Diekhof et al., 2012; Knutson and Greer, 2008; Wilson et al., 2018). Finally, we only included those studies which measured activity during the *prospective* valuation of an action and its rewards, rather than only at the time of reward outcome, as estimates of previously expended effort can be biased by reward receipt (Pooresmaeili et al., 2015).

We contacted the corresponding authors of 28 candidate studies to request whole-brain statistical maps for the analyses of interest, and received whole-brain statistical maps or peak coordinates from 25 studies. In cases where only between-group (e.g. clinical studies) and/or

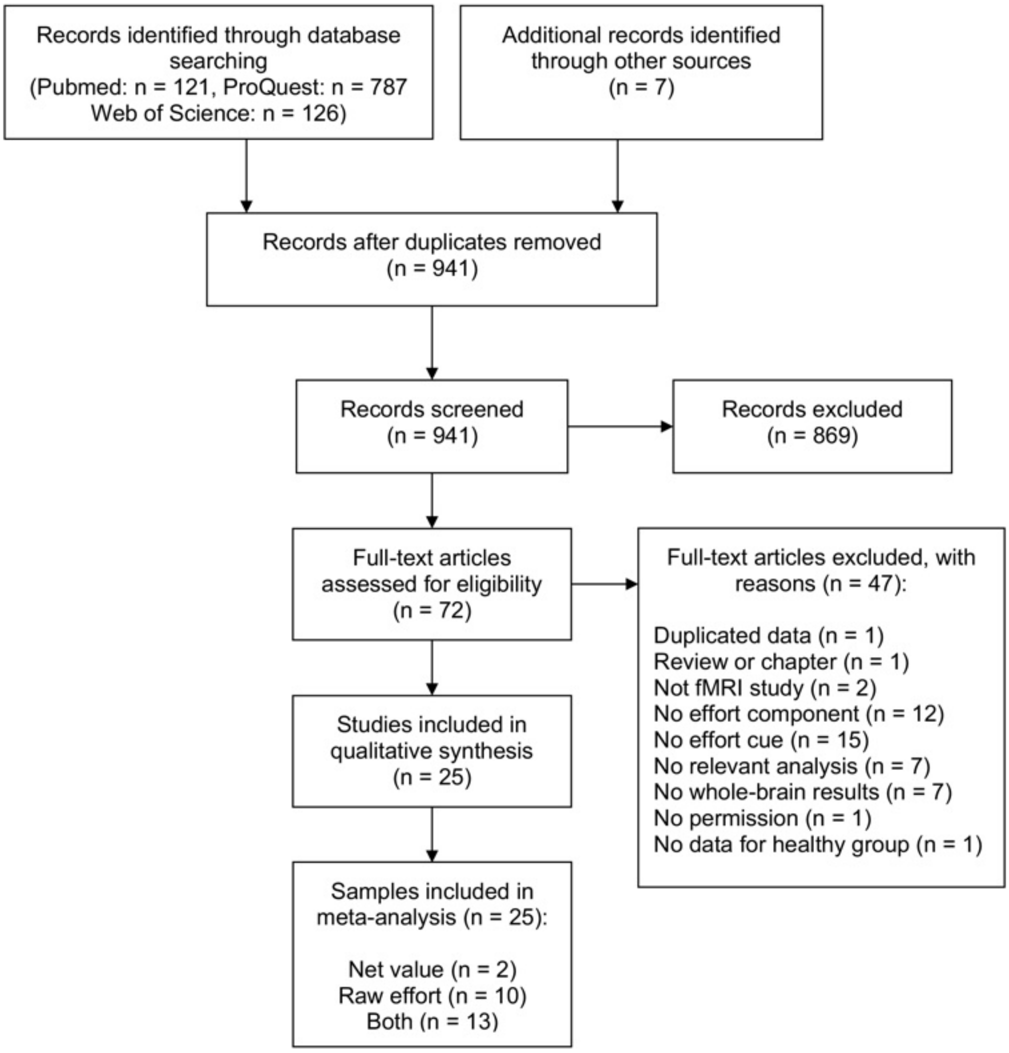


Figure 3.1: Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram.

ROI results were reported, we contacted corresponding authors to inquire about the availability of whole-brain results for relevant contrasts in healthy adult subjects. If images were not available, we requested they provide us with peak foci in stereotactic spatial coordinates (i.e., Talairach or MNI space), together with the direction of the effect (positive or negative).

3.3.1.3 Data collection and preparation

We performed two analyses of interest. The first examined activity related to the raw effort involved in the option itself. We included analyses that examined high vs. low effort demands (i.e., categorical contrasts) and those that examined continuous changes in effort (i.e., parametric modulation). The second analysis examined activity related to the prospective net value of an effortful reward. Whenever possible, we used the contrast related to the net value of a single option (i.e., the subjective value of the chosen option discounted by the effort required to obtain it). When this contrast was unavailable, we used the contrast related to the differences between options instead. Studies that only investigated BOLD activity associated with interactions between reward and effort were excluded, as they did not rely on the same discounting assumptions as other measures of net value. It should be noted that one study (Nagase et al., 2018) included two experiments with six common participants, so we selected the experiment with a larger sample size for the meta-analysis. In another study (Chong et al., 2017), all participants took part in both cognitive and physical effort-based decision-making tasks. Thus, we combined the statistical maps from both tasks to avoid selection bias. Finally, one study (Seaman et al., 2018) had a sample that included participants ranging from 22 to 83 years old. However, the authors of this study provided whole-brain maps that controlled for the effect of age, and we chose to include this data in the net value meta-analysis.

3.3.1.4 Final Corpus

As shown in Figure 3.1, 25 studies were ultimately included in the final corpus of studies, which were considered in one or both meta-analyses on raw effort evaluation and effort-reward integration. The raw effort valuation analysis included 15 maps (65%) and 8 coordinates for raw effort processing, resulting in 23 studies, with a total sample of N = 549 (mean = 24.95; median = 22.5, range = [16-50]). A description of the final corpus of studies can be found in Table 3.1. The net value analysis included 11 maps (73%) and 4 coordinates, resulting in 15 studies, with a total sample of N = 428 participants (mean = 28.5; median = 23, range = [16-75]).

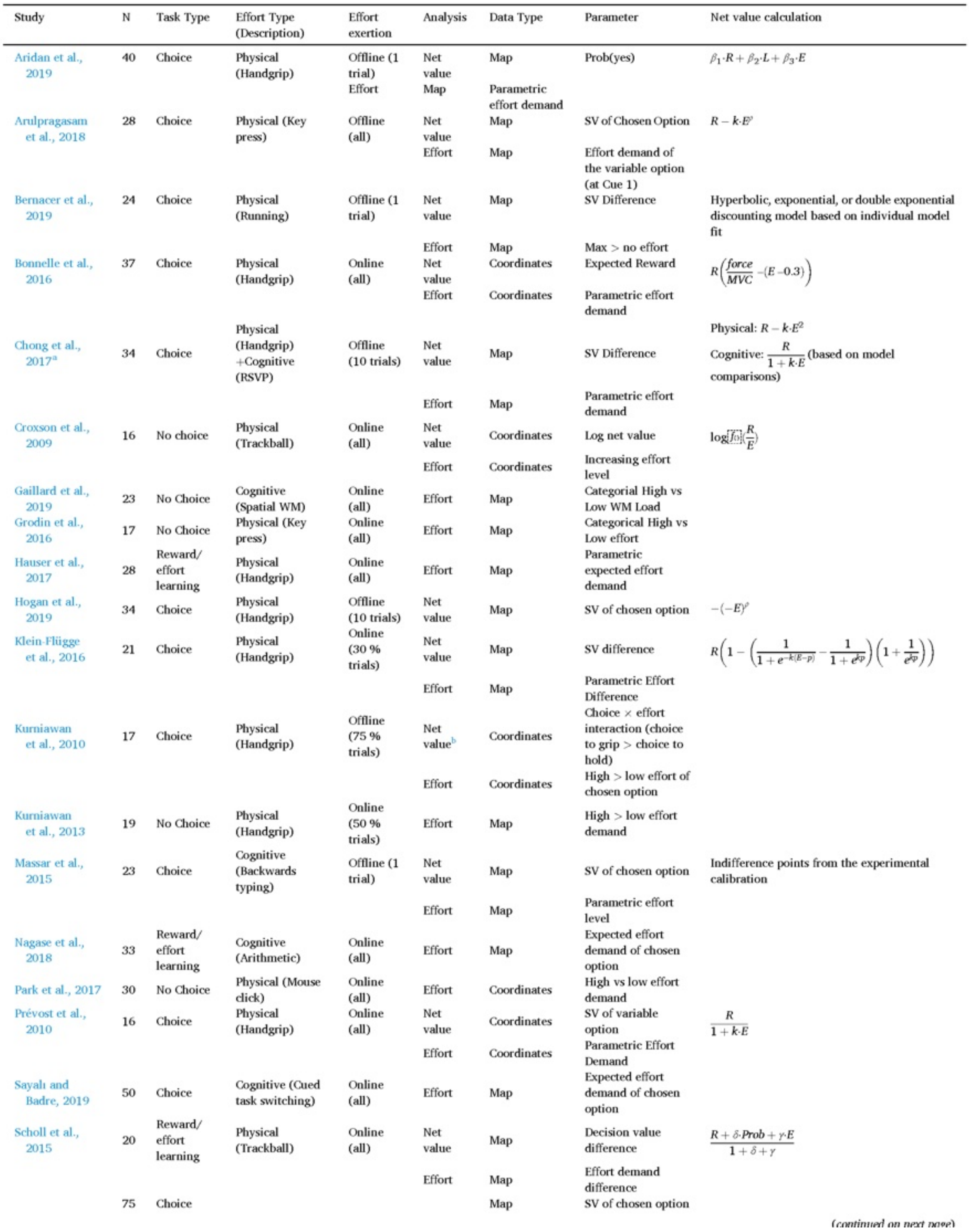
3.3.2 Meta-Analytic Procedures

3.3.2.1 Seed-based d Mapping

Because the inclusion of statistical maps can substantially increase the sensitivity of meta-analyses (Radua et al., 2012), we chose to perform combined image- and coordinate-based meta-analyses using the software Seed-based d Mapping with Permutation of Subject Images (SDM-PSI, version 6.21; https://www.sdmproject.com). SDM-PSI preserves the information about the sign of the effect and the methods have been validated in previous studies (Albajes-Eizagirre et al., 2019; Radua et al., 2012). During preprocessing, SDM-PSI recreated voxel-level maps of standardized effect sizes (i.e., Hedge's g) and their variances and allowed the incorporation of both whole-brain t-maps and peak information (i.e., coordinates and t-values). Specifically, in the case where raw study images were available, effect sizes were estimated from the t, Z, or p values of the map. However, when t-maps were unavailable, SDM-PSI used anisotropic kernels estimate lower and upper effect-sizebounds for each study from reported coordinates and their respective t-values (Radua et al., 2014).

3.3.2.2 Meta-analysis

Two separate whole-brain meta-analyses were conducted to examine consistent neural correlates of prospective effort and net value processing, respectively. SDM-PSI meta-analysis has been described in more detail elsewhere (Albajes-Eizagirre et al., 2019). Briefly, after pre-processing, maximum likelihood estimation (MLE) is used to initially estimate the voxel-wise mean effect sizes and variances. Next, study and subject images were imputed 50 times (Albajes-Eizagirre et al., 2019; Luijten et al., 2017). Using Rubin's rules, SDM-PSI then combines subject images from the different imputations into single combined meta-analysis image. Random-effect models were then used to assess the mean effect size of each study, where the weight of a study is the inverse of the sum of its variance and the between-study variance. SDM Z-maps were generated



Study	N	Task Type	Effort Type (Description)	Effort exertion	Analysis	Data Type	Parameter	Net value calculation
Aridan et al., 2019	40	Choice	Physical (Handgrip)	Offline (1 trial)	Net value	Map	Prob(yes)	$\beta_1 \cdot R + \beta_2 \cdot L + \beta_3 \cdot E$
				Effort	Map	Parametric effort demand		
Arulpragasam et al., 2018	28	Choice	Physical (Key press)	Offline (all)	Net value	Map	SV of Chosen Option	$R - k \cdot E^{p}$
					Effort	Map	Effort demand of the variable option (at Cue 1)	
Bernacer et al., 2019	24	Choice	Physical (Running)	Offline (1 trial)	Net value	Map	SV Difference	Hyperbolic, exponential, or double exponential discounting model based on individual model fit
					Effort	Map	Max > no effort	
Bonnelle et al., 2016	37	Choice	Physical (Handgrip)	Online (all)	Net value	Coordinates	Expected Reward	$R\left(\frac{force}{MVC} - (E - 0.3)\right)$
					Effort	Coordinates	Parametric effort demand	
Chong et al., 2017[a]	34	Choice	Physical (Handgrip) +Cognitive (RSVP)	Offline (10 trials)	Net value	Map	SV Difference	Physical: $R - k \cdot E^2$ Cognitive: $\frac{R}{1 + k \cdot E}$ (based on model comparisons)
					Effort	Map	Parametric effort demand	
Croxson et al., 2009	16	No choice	Physical (Trackball)	Online (all)	Net value	Coordinates	Log net value	$\log \boxed{f()} (\frac{R}{E})$
					Effort	Coordinates	Increasing effort level	
Gaillard et al., 2019	23	No Choice	Cognitive (Spatial WM)	Online (all)	Effort	Map	Categorial High vs Low WM Load	
Grodin et al., 2016	17	No Choice	Physical (Key press)	Online (all)	Effort	Map	Categorical High vs Low effort	
Hauser et al., 2017	28	Reward/ effort learning	Physical (Handgrip)	Online (all)	Effort	Map	Parametric expected effort demand	
Hogan et al., 2019	34	Choice	Physical (Handgrip)	Offline (10 trials)	Net value	Map	SV of chosen option	$-(-E)^{\rho}$
Klein-Flügge et al., 2016	21	Choice	Physical (Handgrip)	Online (30 % trials)	Net value	Map	SV difference	$R\left(1 - \left(\frac{1}{1+e^{-k(E-p)}} - \frac{1}{1+e^{kp}}\right)\left(1 + \frac{1}{e^{kp}}\right)\right)$
					Effort	Map	Parametric Effort Difference	
Kurniawan et al., 2010	17	Choice	Physical (Handgrip)	Offline (75 % trials)	Net value[b]	Coordinates	Choice × effort interaction (choice to grip > choice to hold)	
					Effort	Coordinates	High > low effort of chosen option	
Kurniawan et al., 2013	19	No Choice	Physical (Handgrip)	Online (50 % trials)	Effort	Map	High > low effort demand	
Massar et al., 2015	23	Choice	Cognitive (Backwards typing)	Offline (1 trial)	Net value	Map	SV of chosen option	Indifference points from the experimental calibration
					Effort	Map	Parametric effort level	
Nagase et al., 2018	33	Reward/ effort learning	Cognitive (Arithmetic)	Online (all)	Effort	Map	Expected effort demand of chosen option	
Park et al., 2017	30	No Choice	Physical (Mouse click)	Online (all)	Effort	Coordinates	High vs low effort demand	
Prévost et al., 2010	16	Choice	Physical (Handgrip)	Online (all)	Net value	Coordinates	SV of variable option	$\frac{R}{1 + k \cdot E}$
					Effort	Coordinates	Parametric Effort Demand	
Sayalı and Badre, 2019	50	Choice	Cognitive (Cued task switching)	Online (all)	Effort	Map	Expected effort demand of chosen option	
Scholl et al., 2015	20	Reward/ effort learning	Physical (Trackball)	Online (all)	Net value	Map	Decision value difference	$\frac{R + \delta \cdot Prob + \gamma \cdot E}{1 + \delta + \gamma}$
					Effort	Map	Effort demand difference	
	75	Choice				Map	SV of chosen option	

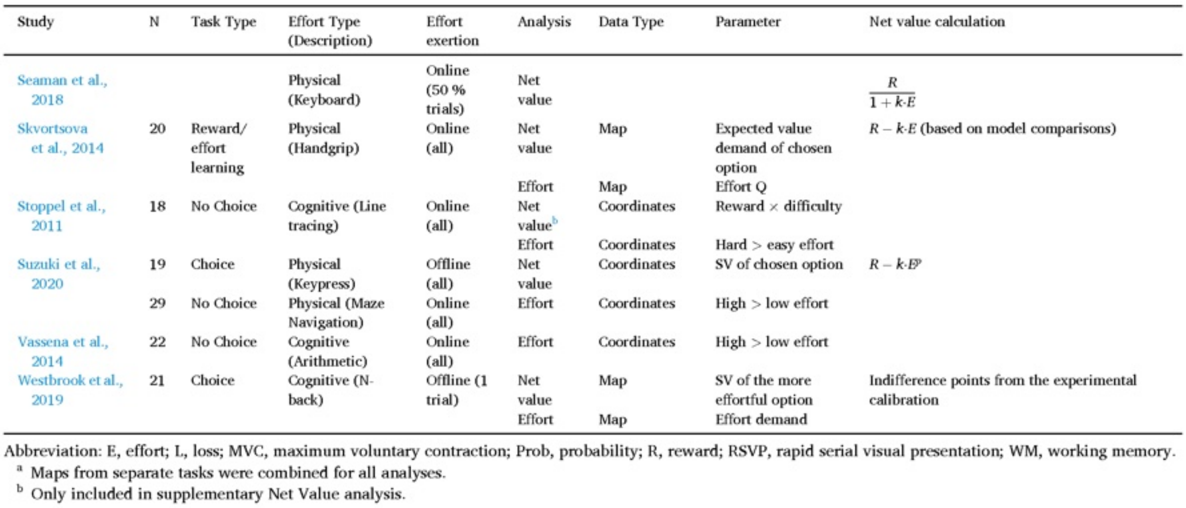
(continued on next page)

Table 3.1: Summary of Included Studies. Abbreviation: E, effort; L, loss; MVC, maximum voluntary contraction; Prob, probability; R, reward; RSVP, rapid serial visual presentation; WM, working memory.

[a] Maps from separate tasks were combined for all analyses.

[b] Only included in supplementary Net Value analysis.

by dividing the voxel-wise effect sizes by their standard errors. As these Z-values may deviate from a normal distribution, a null-distribution was estimated for each meta-analysis from 50 whole-brain permutations, as is standard in SDM-PSI.



Study	N	Task Type	Effort Type (Description)	Effort exertion	Analysis	Data Type	Parameter	Net value calculation
Seaman et al., 2018			Physical (Keyboard)	Online (50 % trials)	Net value			$\frac{R}{1+k \cdot E}$
Skvortsova et al., 2014	20	Reward/ effort learning	Physical (Handgrip)	Online (all)	Net value	Map	Expected value demand of chosen option	$R - k \cdot E$ (based on model comparisons)
					Effort	Map	Effort Q	
Stoppel et al., 2011	18	No Choice	Cognitive (Line tracing)	Online (all)	Net value[b]	Coordinates	Reward × difficulty	
					Effort	Coordinates	Hard > easy effort	
Suzuki et al., 2020	19	Choice	Physical (Keypress)	Offline (all)	Net value	Coordinates	SV of chosen option	$R - k \cdot E^p$
	29	No Choice	Physical (Maze Navigation)	Online (all)	Effort	Coordinates	High > low effort	
Vassena et al., 2014	22	No Choice	Cognitive (Arithmetic)	Online (all)	Effort	Coordinates	High > low effort	
Westbrook et al., 2019	21	Choice	Cognitive (N-back)	Offline (1 trial)	Net value	Map	SV of the more effortful option	Indifference points from the experimental calibration
					Effort	Map	Effort demand	

Abbreviation: E, effort; L, loss; MVC, maximum voluntary contraction; Prob, probability; R, reward; RSVP, rapid serial visual presentation; WM, working memory.

[a] Maps from separate tasks were combined for all analyses.

[b] Only included in supplementary Net Value analysis.

Region-of-Interest (ROI) Analysis. To directly investigate the involvement of key brain regions in effort-related cost processing and value integration, we focused on seven a priori regions of interest (ROIs) derived from an independent meta-analysis (Bartra et al., 2013) that examined valuation network in general. Those ROIs included: the vmPFC, right and left VS, ACC, pre-SMA, and right and left AI, which generally covered the core valuation network and additional frontal regions of interest. A spherical mask of radius 6mm was created for each ROI centered on the respective peak coordinates. Effect sizes and variances of those ROIs were extracted from each study and plotted as forest plots. We used the metafor package (Viechtbauer, 2010) in R version 4.0.3 (https://www.r-project.org) to calculate mean effect sizes and 95% confidence intervals for each ROI, as this package allows for specification of variance estimates from each study.

Whole-Brain Analysis. We also examined the whole-brain results beyond these a priori ROIs. To reduce the false-positive results due to multiple comparisons, we applied a familywise error (FWE) correction with 1000 subject-based permutations (Albajes-Eizagirre et al., 2019). In accordance with SDM-PSI's recommendations, a threshold-free cluster enhancement (TFCE) corrected $p<0.025$ was used (Albajes-Eizagirre et al., 2019).

In addition, we performed a conjunction analysis to identify regions that were associated with both raw effort demand and net value. For exploratory purposes, we created maps using a voxel-level uncorrected threshold of $p<0.001$ and a cluster size>20 voxels for both meta-analyses. Masks were generated from significant clusters scaled positively or negatively with either raw effort demand or net value (i.e., based on absolute values). We then used SPM12 (http://www.fil.ion.ucl.ac.uk/spm) to perform a conjunction analysis to extract overlapping areas for both processes, regardless of the direction (Cutler and Campbell-Meiklejohn, 2019).

Because of the high level of heterogeneity of task features and parameters between studies, we were interested in assessing if our findings were driven by a specific design. Specifically, tasks varied in effort type (i.e. cognitive effort vs. physical effort), probability of effort execution (online vs offline effort), and net value parameter (single net value vs. value difference between two options). However, direct comparisons would be underpowered, as too few studies contained specific task features. Thus, in order to explore if studies with certain task features showed patterns of activity that were unique and/or overlapping to activations patterns identified in the main analyses, we conducted 6 supplementary meta-analyses using subgroups of studies ($N \geq 10$ studies in a subgroup) from the main raw effort and net value analyses.

First, in order to identify regions involved in signaling prospective physical effort demands and integration of physical effort costs with reward, we repeated both raw effort and net value analyses with a subgroup of studies using physical effort tasks (N=16 and N=13, respectively). Note in the case of studies that had both physical and cognitive effort tasks (i.e. Chong et al. (2017)), only maps from the physical effort task were used.

Second, in many effort-based decision-making studies, subjects were required to either execute the effort immediately after a choice (i.e., online execution) or execute the effort (or a random sample) at the end of the task (i.e., offline execution). Thus, to examine if regions consistently engaged in raw effort valuation overlapped with regions involved in signaling purely immediate effort requirements, we conducted a sub-group analysis that investigated prospective effort signaling in tasks using real online effort (N= 16).

Third, because of the possible role of the dorsal ACC and other frontal regions in signaling choice difficulty, we were interested in assessing if our findings were influenced by studies that used net value differences as the parameter, rather than the net value of the chosen option. Thus, we repeated the meta-analysis with a subgroup of studies that used parameters only representing the net value of a single option ($N = 11$).

Fourth, because net value can also be more broadly defined as an interaction between reward and effort, we repeated the net value meta-analysis by including the coordinates of two additional studies (Kurniawan et al., 2010; Stoppel et al., 2011) that used interaction parameters (e.g. Reward X Effort) as opposed to traditional discounting parameters of net value (e.g. SV).

Finally, although the neural correlates of raw reward have been widely examined in previous studies (e.g., Bartra et al., 2013; Sescousse et al., 2013), for the confirmatory purpose, we conducted a raw reward analysis based on studies that examined reward processing ($N = 13$). These analyses were conducted using the same procedures described above.

3.3.2.3 Heterogeneity and Publication Bias

Significant clusters were assessed for heterogeneity, or the degree of between-study variance due to other factors (e.g. differences in analytical approaches, subject populations, etc.) aside from random error. For each meta-analysis, peaks with heterogeneity I^2 values >20% were flagged and inspected. Although it has been suggested that I^2 statistics are inflated in small sample meta-analyses (Von Hippel, 2015), we note any clusters with high I2 values >20%, values, as results from these clusters may be driven by other factors rather than chance.

Publication bias, or the favoring of publishing significant, as opposed to null, findings, can inflate meta-analysis effect sizes. In order to assess publication bias, we created funnel plots for peak voxels of significant clusters in which Hedge's g effect size estimates were plotted against a measure of precision (i.e. variance of Hedge's g estimate). Funnel plots for each cluster were visually inspected for asymmetry, which would suggest that reported effect sizes are related to their statistical significance. For each significant cluster, Egger regression tests (Egger et al., 1997) were also conducted to quantitatively test if the number of studies with statistically significant results is larger than expected. Significant results in an Egger regression would indicate the possible existence of unpublished studies with non-significant effects. These statistics are reported alongside the effect sizes for each significant cluster.

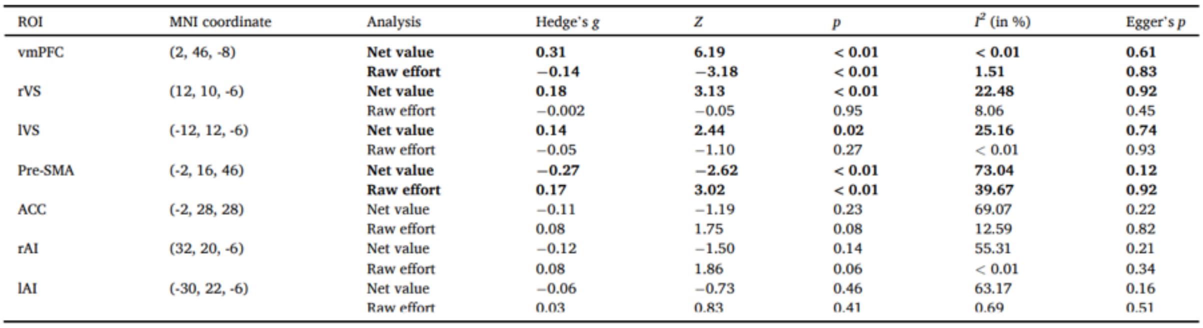
3.3.3 Data Availability

The protocol for this study was not pre-registered. However, unthresholded Z-maps of our results are available at NeuroVault: https://neurovault.org/collections/9286/. The TFCE-corrected maps as well as publication bias and heterogeneity data are available from the corresponding authors upon request.

3.4 Results

3.4.1 ROI Analysis

To directly examine the roles of key regions in raw effort prospect and effort-reward integration, we focused on seven *a priori* ROIs. Results are summarized in Table 3.2. The vmPFC consistently showed positive associations with net value and negative associations with raw effort. The bilateral VS showed a similar response pattern, but smaller effect sizes for both analyses. In contrast, the pre-SMA scaled positively with raw effort and, albeit more variably, negatively with net value. The ACC and bilateral AI showed a similar response pattern, but smaller effect sizes for both analyses. Figures 3.2 and 3.3 show the Hedge's g effect sizes for raw effort and net value analyses in the vmPFC and pre-SMA ROIs. The forest plots for other regions were shown in Figure 3.S1- 3.S10. To statistically test the opposite response patterns of the vmPFC and pre-SMA, we focused on studies with both raw effort and net value data (N = 13) and conducted a linear mixed-effects model with Measure (Effort and Net Value), Region (vmPFC and pre-SMA), and their interaction as fixed effects, study as a random effect, and Hedge's g effect



ROI	MNI coordinate	Analysis	Hedge's g	Z	p	I^2 (in %)	Egger's p
vmPFC	(2, 46, -8)	**Net value**	**0.31**	**6.19**	**< 0.01**	**< 0.01**	**0.61**
		Raw effort	**−0.14**	**−3.18**	**< 0.01**	**1.51**	**0.83**
rVS	(12, 10, -6)	**Net value**	**0.18**	**3.13**	**< 0.01**	**22.48**	**0.92**
		Raw effort	−0.002	−0.05	0.95	8.06	0.45
lVS	(-12, 12, -6)	**Net value**	**0.14**	**2.44**	**0.02**	**25.16**	**0.74**
		Raw effort	−0.05	−1.10	0.27	< 0.01	0.93
Pre-SMA	(-2, 16, 46)	**Net value**	**−0.27**	**−2.62**	**< 0.01**	**73.04**	**0.12**
		Raw effort	**0.17**	**3.02**	**< 0.01**	**39.67**	**0.92**
ACC	(-2, 28, 28)	Net value	−0.11	−1.19	0.23	69.07	0.22
		Raw effort	0.08	1.75	0.08	12.59	0.82
rAI	(32, 20, -6)	Net value	−0.12	−1.50	0.14	55.31	0.21
		Raw effort	0.08	1.86	0.06	< 0.01	0.34
lAI	(-30, 22, -6)	Net value	−0.06	−0.73	0.46	63.17	0.16
		Raw effort	0.03	0.83	0.41	0.69	0.51

Table 3.2: Results of ROI Analysis. Abbreviations: ACC, anterior cingulate cortex; AI, anterior insula; l, left; r, right, vmPFC, ventromedial prefrontal cortex; VS, ventral striatum. The significant results are indicated in bold font.

sizes as the dependent variable. As expected, the analysis identified a significant interaction between Measure and Region (β= -0.83, Z = -7.16, p<0.001), such that, for vmPFC, effect sizes were more positive for net value than effort. Conversely, for pre-SMA, effect sizes more positive for effort than net value (see Table 3.S1 and Figure 3.S11).

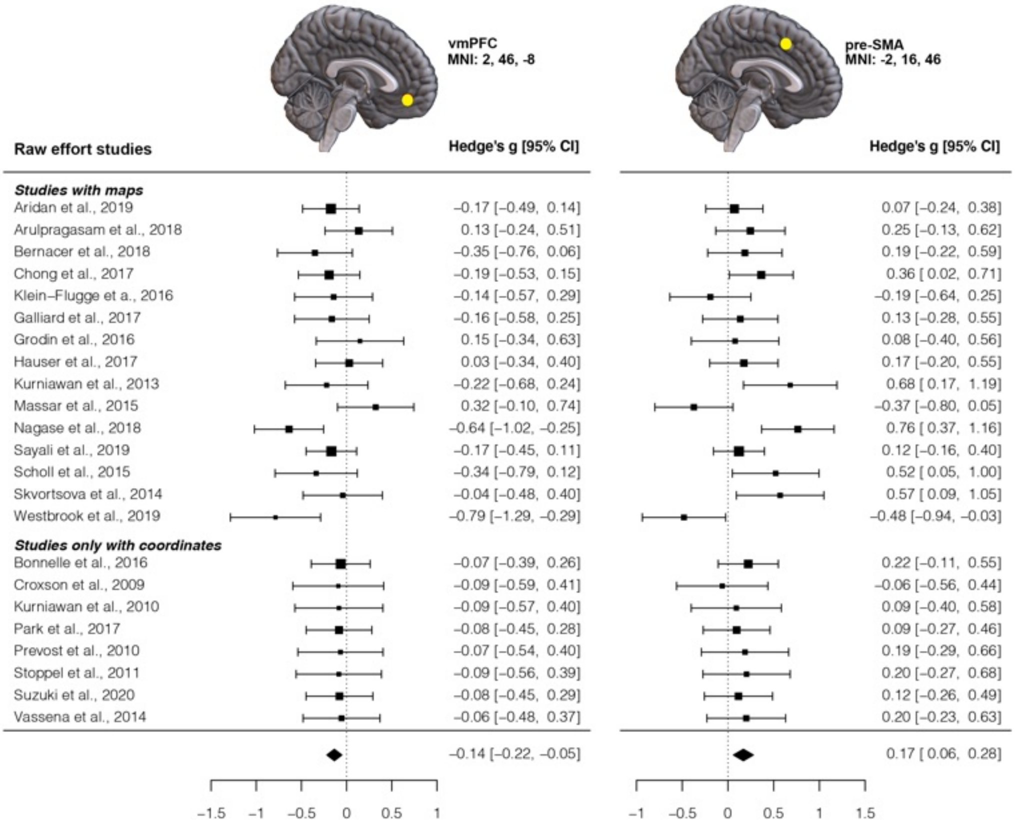


Figure 3.2: Forest plot illustrating activation related to effort demand in the vmPFC and pre-SMA ROIs in studies with statistical maps. The pre-SMA is positively associated with raw effort (Hedge's g= 0.20, 95% CI [0.02, 0.37]), whereas the vmPFC showed a negative association (Hedge's g= -0.17, 95% CI [-0.30, -0.03]).

Finally, to explore the hierarchical structure of the seven ROIs during raw effort and net value processing, we examined the correlations between effect sizes of these regions across studies. As shown in Figure 3.S12, the correlation map for the raw effort analysis revealed two distinct networks, with one including the vmPFC and bilateral VS, and the other including the pre-SMA, ACC, and bilateral AI. The pattern is less clear for the net value analysis (Figure 3.S13), where the vmPFC activity did not show strong correlations with other regions, possibly due to its low variance (i.e., high consistency) across studies. Other regions showed high correlations across studies. These findings further suggest that the vmPFC and pre-SMA may play opposite roles in effort-related cost encoding and net value computation, although the correlation maps identified here are complex and more evidence is still needed to elucidate how these regions interact with each other during effort-based valuation.

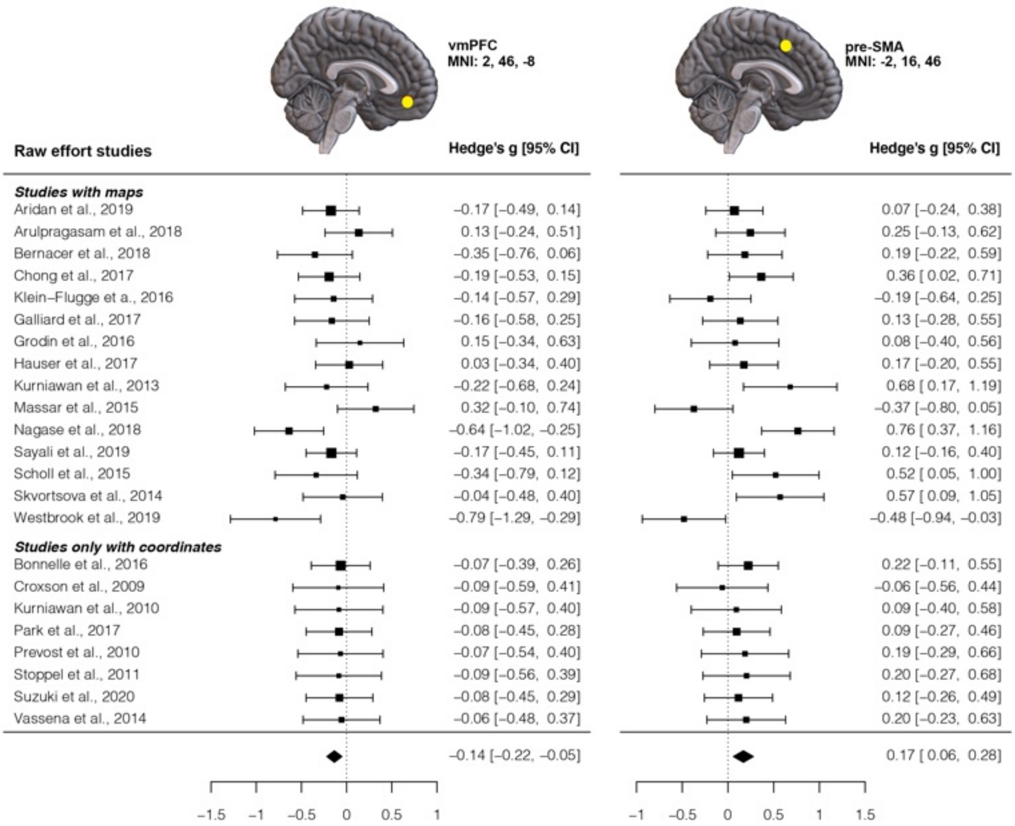


Figure 3.3: Forest plot illustrating activation related to net value in the vmPFC and pre-SMA ROIs in studies with statistical maps. The vmPFC is positively associated with net value (Hedge's g= 0.22, 95% CI [0.22, 0.44]), whereas the pre-SMA showed a negative association (Hedge's g= -0.28, 95% CI [-0.52, -0.03]).

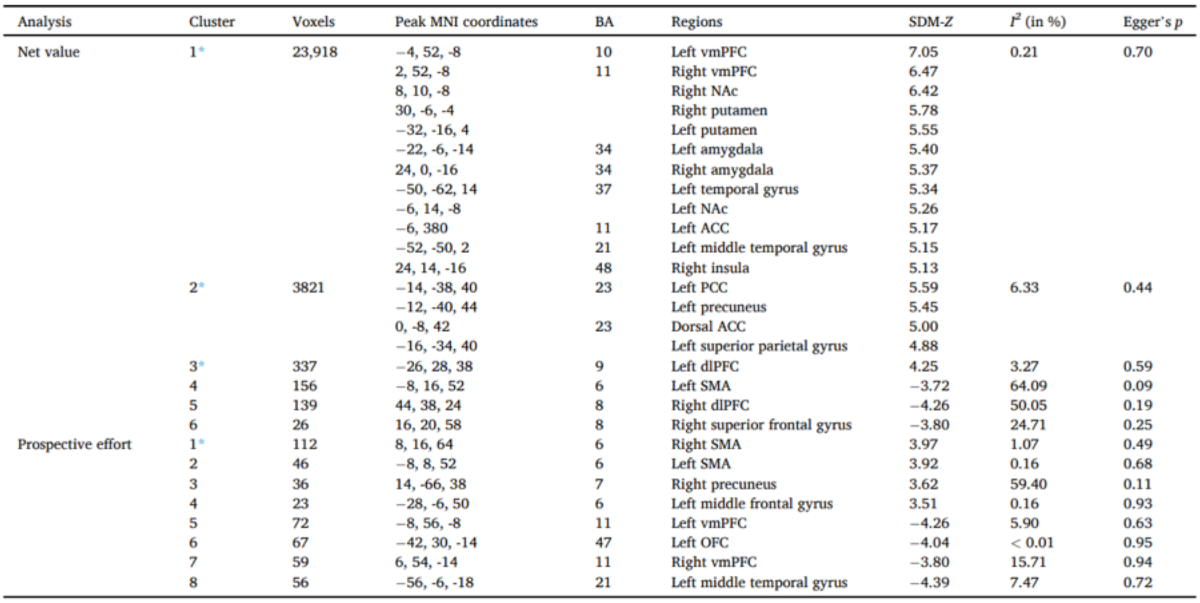
3.4.2 Whole-Brain Analysis

3.4.2.1 Raw Effort

We first examined brain regions that were consistently associated with raw effort processing. As illustrated in Figure 3.4a, the analysis yielded positive effects clustered in the right pre-SMA and adjacent caudal ACC (see Table 3.3). At a more lenient, uncorrected $p<0.001$ threshold, other positive foci were detected in the left SMA, right precuneus, and left middle frontal gyrus, and negative foci were detected in the bilateral vmPFC/OFC and left middle temporal gyrus. Heterogeneity I^2 statistics, funnel plots and Egger regressions did not detect excess heterogeneity or publication bias in any significant clusters in the TFCE-corrected findings. However, in the uncorrected analysis, a cluster in the right precuneus was found to be associated with extreme heterogeneity (I^2 = 59.50%).

3.4.2.2 Net Value

Next, we examined brain regions that were consistently associated with net value encoding. As illustrated in Figure 3.4b, the analysis yielded a large cluster connecting cortical and subcortical regions of the medial PFC, VS, dorsal striatum (bilateral putamen and left caudate), and temporal gyrus (see Table 3.3). Moreover, a cluster consisting of the bilateral medial and posterior cingulate cortex and precuneus and a separate cluster in the left middle frontal gyrus also showed significantly positive associations. Some small clusters, including the left SMA, right dorsolateral PFC (dlPFC), and right superior frontal gyrus, scaled negatively with net value, although these results were only detectable at a lenient uncorrected p<0.001 threshold.



Analysis	Cluster	Voxels	Peak MNI coordinates	BA	Regions	SDM-*Z*	I^2 (in %)	Egger's *p*
Net value	1*	23,918	−4, 52, -8	10	Left vmPFC	7.05	0.21	0.70
			2, 52, -8	11	Right vmPFC	6.47		
			8, 10, -8		Right NAc	6.42		
			30, -6, -4		Right putamen	5.78		
			−32, -16, 4		Left putamen	5.55		
			−22, -6, -14	34	Left amygdala	5.40		
			24, 0, -16	34	Right amygdala	5.37		
			−50, -62, 14	37	Left temporal gyrus	5.34		
			−6, 14, -8		Left NAc	5.26		
			−6, 380	11	Left ACC	5.17		
			−52, -50, 2	21	Left middle temporal gyrus	5.15		
			24, 14, -16	48	Right insula	5.13		
	2*	3821	−14, -38, 40	23	Left PCC	5.59	6.33	0.44
			−12, -40, 44		Left precuneus	5.45		
			0, -8, 42	23	Dorsal ACC	5.00		
			−16, -34, 40		Left superior parietal gyrus	4.88		
	3*	337	−26, 28, 38	9	Left dlPFC	4.25	3.27	0.59
	4	156	−8, 16, 52	6	Left SMA	−3.72	64.09	0.09
	5	139	44, 38, 24	8	Right dlPFC	−4.26	50.05	0.19
	6	26	16, 20, 58	8	Right superior frontal gyrus	−3.80	24.71	0.25
Prospective effort	1*	112	8, 16, 64	6	Right SMA	3.97	1.07	0.49
	2	46	−8, 8, 52	6	Left SMA	3.92	0.16	0.68
	3	36	14, -66, 38	7	Right precuneus	3.62	59.40	0.11
	4	23	−28, -6, 50	6	Left middle frontal gyrus	3.51	0.16	0.93
	5	72	−8, 56, -8	11	Left vmPFC	−4.26	5.90	0.63
	6	67	−42, 30, -14	47	Left OFC	−4.04	< 0.01	0.95
	7	59	6, 54, -14	11	Right vmPFC	−3.80	15.71	0.94
	8	56	−56, -6, -18	21	Left middle temporal gyrus	−4.39	7.47	0.72

Table 3.3: Results of Whole Brain Analyses. All results survived a statistical threshold of voxel-level uncorrected p <0.001 and cluster size >20. Abbreviations: BA, Brodmann areas; vm, ventromedial; dl, dorsolateral; d, dorsal; r, rostral; PFC, prefrontal cortex; NAc, nucleus accumbens; ACC, anterior cingulate cortex; PCC, posterior cingulate cortex; SMA, supplementary motor area; OFC, orbitofrontal cortex.
*Regions survived a statistical threshold of TFCE-corrected p <0.025.

In addition, heterogeneity I^2 statistics, funnel plots and Egger regressions showed no evidence of excess heterogeneity or publication bias in any of the significant clusters for the main net value or single SV subgroup TFCE-corrected results. No evidence of publication bias was detected in the uncorrected net value analysis, however negative clusters the left SMA and right dlPFC had I^2 statistics of 64.09% and 50.05% respectively, suggesting that findings in these two regions were highly heterogenous.

3.4.2.3 Conjunction Analysis

Finally, we performed a conjunction analysis to identify areas that are sensitive to both net value and effort requirements. Due to the exploratory nature of this analysis, we used a lenient threshold of uncorrected p<0.001 at voxel level and k >20 at cluster level. Note that we used absolute values in the conjunction analysis because of the opposite response pattern found in the main prospective effort and net value meta-analyses. We found that the vmPFC and left lateral orbitofrontal cortex scaled positively with net value and negatively with effort requirement. The response pattern was reversed in the pre-SMA and caudal ACC (Figure 4c). However, these findings were not detectable after whole-brain TFCE-correction.

3.4.2.4 Supplementary Analyses

Raw Effort, Physical Effort subgroup. Findings generally overlapped with the main raw effort analysis. The analysis yielded one cluster in the bilateral precuneus and PCC and extend-

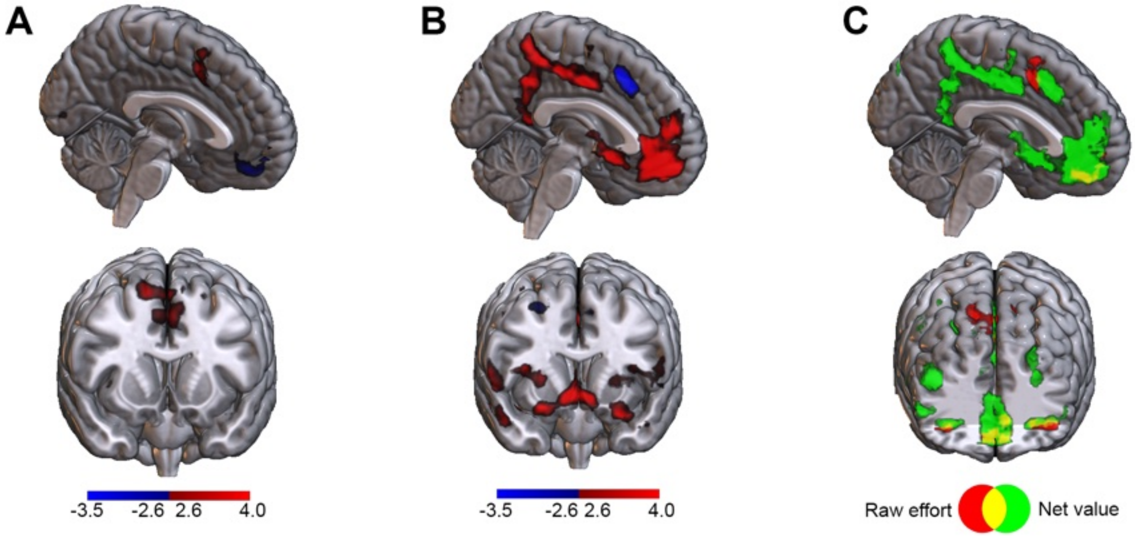


Figure 3.4: Whole-brain meta-analytic results. A: neural activity related to pure effort cost representation; B: neural activity related to net value; and C: their conjunction based on absolute values. Display threshold: uncorrected p<0.005 at voxel level.

ing towards the right supramarginal gyrus, another in the bilateral SMA and dACC, and a third, small cluster in the right frontal pole and dlPFC that were consistently positively associated with physical effort demands (see Table 3.S2 and Figure 3.S14). However, unlike the original raw effort meta-analysis, negative association in the vmPFC not significant.

Net Value, Physical Effort subgroup. Similar to the main net value analysis, BOLD activity in the mOFC, vmPFC, and rostral ACC, PCC and striatum was positively associated with the net value in studies measuring physical effort (see Table 3.S3 and Figure 3.S15). Negative effects were also detected; however, they were associated with high heterogeneity (all I^2 >40%).

Raw Effort, Online Execution. Similar to the main prospective effort analysis, BOLD activity in the bilateral pre-SMA and ACC was positively associated with effort demand in studies requiring effort execution during the task (Table 3.S4 and Figure 3.S16).

Other Metrics of Net Value. To ensure that the results of the net value meta-analysis were not driven by choice difficulty, we reran our analysis excluding four experiments that used the value of two options as their net value metric (e.g. difference in SV of more vs less effortful option). Importantly, the vmPFC and bilateral VS remained to be the foci with highest effect sizes, and the whole-brain activation pattern was qualitatively similar (see Table 3.S5 and Figure 3.S17), suggesting that our main findings were not influenced by the cognitive demands of comparing two options. Moreover, to ensure that our findings were robust when using a broader definition of net value, we also repeated our analysis including two additional studies that used reward and effort interactions as a measure of net value. Main foci and whole-brain activation patterns remained qualitatively similar to the initial net value meta-analysis (see Table 3.S6 and Figure 3.S18). However, deactivations associated with net value were not detected in these supplementary analyses, suggesting that the deactivations in the SMA detected in the main meta-analysis were not robust.

Raw Reward. The results showed that the activity of a large cluster, including the vmPFC, bilateral VS, DS, PCC, ACC, and some occipital regions, was positively associated with raw reward magnitude. These results largely overlapped with clusters identified in the net value analysis (Table 3.S7 and Figure 3.S19).

3.5 Discussion

We conducted a series of combined coordinate- and image-based meta-analyses to examine the neural substrates of effort-based valuation. We first investigated neural activity related to raw effort and net value in seven a priori ROIs previously implicated in value-based decision-making. We found these regions could be broadly divided into two groups that exhibited distinct activity pattern during these two processes, with the vmPFC and pre-SMA as the central node of each. Specifically, the vmPFC scaled positively with net value but negatively with raw effort, whereas the pre-SMA displayed the opposite pattern. The exploratory whole-brain and conjunction analyses further corroborate the ROI analyses. These findings provide strong evidence for different, yet complementary, roles of the vmPFC and pre-SMA in the valuation of effort costs, and implicate these two regions as core components of a network that drives motivated behavior.

Our findings provide comprehensive evidence that effort-related net value integration is processed in a network centered around the vmPFC and VS. Accumulating evidence implicates the vmPFC as a general hub for value integration, as it has been identified to signal net value of rewards across different cost domains, such as risk and delay (Croxson et al., 2009; Hogan et al., 2019; Kable and Glimcher, 2007; I. Levy et al., 2010; Peters and Büchel, 2009; Schmidt et al., 2012; Westbrook et al., 2019. Additionally, the network including the vmPFC has been implicated in tracking net values across reward domains (i.e., primary, secondary, and aesthetic rewards), reward processing phases (Bartra et al., 2013; Clithero and Rangel, 2014; D. J. Levy and Glimcher, 2012; Sescousse et al., 2013), reward rates, and the value of current and previous offers Mehta et al., 2019. These findings are therefore consistent with prominent neuroeconomic accounts which propose that the vmPFC represents the net value of an option in a ‘common currency’, in order to facilitate value comparison during decision making (Padoa-Schioppa, 2011; Rangel et al., 2008; Westbrook and Braver, 2015).

One would hypothesize that a region involved in representing net value would negatively scale with effort demands. Except for the vmPFC, our study did not find that other net-value-related regions, such as the VS, meet this requirement. These findings are at odds with previous reports that the VS activity is negatively modulated by effort costs in the presence of reward information (Westbrook et al., 2019). Moreover, dorsal parts of the striatum have also been found to track both effort costs (“Action controls dopaminergic enhancement of reward representations.”, 2012; Burke et al., 2013; hua Yang et al., 2016; Klein-Flugge et al., 2016; Kurniawan et al., 2010; Kurniawan et al., 2013) and net value of prospective effortful rewards (Klein-Flugge et al., 2016; Seaman et al., 2018). However, our results implicate motor-related regions of the striatum, particularly the putamen, as signaling net value alone. One plausible explanation is that the striatum signals reward information during the evaluation of prospective effortful rewards (which we focused on in the current study) and encodes effort costs during the initiation of an effortful action (Suzuki et al., 2021). In line with this, studies that have experimentally isolated prospective effort and reward cues showed that the striatum was not activated by effort alone during the anticipation phase (Arulpragasam et al., 2018). However, future investigations that examine the role of the striatum during different time windows are needed to directly test this hypothesis.

The PCC also showed a reliable association with net value, but not effort requirement. Along with the vmPFC, the PCC is a critical node of the default mode network (Acikalin et al., 2017). It has also been considered as a key component of the valuation system in other cost domains (Bartra et al., 2013; Clithero and Rangel, 2014; Peters and Büchel, 2009). Its precise role in effort-based valuation remains largely unclear, but it has been implicated in monitoring temporal changes to the environment (Pearson et al., 2011) or integrating changes to the internal and external environment (Nakao et al., 2012), Moreover, previous studies have shown that the activity of the PCC was positively associated with the degree of uncertainty during value-based decision-making (McCoy and Platt, 2005). Taken together, the PCC may play a role in transmitting the background information to the vmPFC to guide the net value calculation, although it remained to be tested by studies that dissociate net value and these components.

Finally, both main and supplementary analyses consistently identified a variety of parietotemporal regions as scaling positively and uniquely with net value representations. While these regions (i.e. intraparietal lobule, intraparietal sulcus, temporal pole, etc.) have been previously implicated in SV encoding of effortful rewards (Chong et al., 2017; Massar et al., 2015), they also play a critical role in perceptual decision-making (Keuken et al., 2014), attention (Husain, 2019), risk weighting (Mohr et al., 2010), and decision difficulty (Westbrook et al., 2019). Their notable absence in reward processing (Keuken et al., 2014; Sescousse et al., 2013 may thus suggest that these parietotemporal regions are involved in high-level perceptual and cognitive functions associated with task demands as opposed to net value computation.

Previous studies have identified effort-related net value signals in other frontal regions, such as the pre-SMA and ACC, which suggests that these regions may be specifically relevant for effort-reward integration. In the current meta-analysis, however, we found that these regions —in particular, the pre-SMA and adjacent caudal ACC —all scaled positively with raw effort costs and, albeit less robustly, scaled negatively with net value. Such a pattern suggests that these regions are more likely to be involved in the processing of effort-related costs, rather than value integration per se. These findings align closely with a previous transcranial magnetic stimulation study, in which disruption of the SMA led to decreased effort perception (Zénon et al., 2015). The pre-SMA and dorsal ACC are also recruited to process other types of costs, such as risk (Mohr et al., 2010) and delay (Schüller et al., 2019). A plausible mechanism, therefore, is that these regions serve as a domain-general hub for cost encoding and transfer the cost information to the vmPFC for calculation of net value. Alternatively, neuroeconomic models of effort-based decision-making have posited that the ACC, in particular, is involved in good-to-action transformation (Padoa-Schioppa, 2011). Thus, another plausible mechanism is that the vmPFC computes and compares the net value of separate options and passes choice preference to action selection regions, such as the pre-SMA and ACC, for conversion to motor output.

Despite strong evidence about the involvement of the caudal ACC, which is close to the pre-SMA, in effort costs processing, it should be noted that the ACC, as a whole, is highly heterogeneous (Neubert et al., 2015; Yu et al., 2011). Indeed, the whole-brain results showed distinct response patterns across the ACC, in which the ventral part was mainly involved in net value computation, whereas the dorsal part in raw effort encoding. These findings suggest that subregions of the ACC could be linked to different aspects of the effort-related valuation, which may also partly explain the fact that some studies identified net value signals in the ACC (Klein-Flugge et al., 2016; Massar et al., 2015). Moreover, net-value-related activation may emerge in the dorsal ACC if it is highly correlated with other confounding variables, such as decision difficulty (Shenhav et al., 2013). It is particularly plausible for studies that have used the SV difference between two options as the net value parameter, as it often approximates decision difficulty (Klein-Flugge et al., 2016). Notably, studies that have experimentally isolated net value and decision difficulty showed that the cognitive control network, including the dorsal ACC and other frontoparietal regions, tracked the latter but not the former (Hogan et al., 2019; Westbrook et al., 2019).

The current study has some limitations. First, the sample size of the net value analysis is relatively small. Although the inclusion of statistical images partly offsets this issue, the number of included studies did not allow for us to perform meta-regressions, which would have provided more conclusive answers about the effects of potential moderators, such as effort type (i.e., physical vs. cognitive), parameter type (i.e., difference in SV vs. SV of one option), and effort execution requirement (i.e., real vs. hypothetical). These secondary analyses could be particularly relevant for understanding less consistent effects, such as the ones detected here in the pre-SMA ROI. Specifically, it is unclear if the high degree of heterogeneity in our net value effect size estimates in the pre-SMA ROI were due to differences in preparatory motor activity between tasks, selective networks engaged for cognitive vs. physical effort, or other unobserved factors, such as individual differences. Furthermore, sub-group meta-analyses investigating effects of different reward schedules (e.g., cumulative vs. random payout) were underpowered. Thus, we were unable to disambiguate between pure reward/effort integration and encoding of probabilistic features of the individual tasks. This is particularly important for effects observed in the PCC, OFC, and mPFC, as these regions have been consistently involved in signaling prospective reward uncertainty (Bailey et al., 2016; Burke et al., 2013; Dreher, 2013; Peters and Büchel, 2009; Prévost et al., 2010). Given the sensitivity of effort-based decisions to both reward probability (Barch et al., 2014; Soder et al., 2020; M. T. Treadway, Buckholtz, et al., 2012) and opportunity costs (Otto and Daw, 2019), future research should directly explore the interaction between effort demand and other cost domains and/or task features. Second, the majority of the included studies focused on physical effort. These findings should be treated cautiously when generalizing to other formats of effort. Finally, the meta-analytic results reflected consistent regional neural correlates across studies. Although our study identified critical brain regions related to effort-related value integration or cost encoding, how these regions interact with each other to achieve the dynamic valuation process remains to be elucidated by studies using task-based connectivity technique (Hauser et al., 2017) or imaging methods with higher temporal resolution (e.g., magnetoencephalography).

In conclusion, this study is the first to use combined image- and coordinate-based meta-analyses to examine neural activity related to effort-related costs and net value. The results showed the pre-SMA is involved in cost representation of prospective effort independent of rewards. In contrast, the vmPFC and VS, which have been implicated in value integration in other cost domains, are also involved in effort-reward integration. These findings further clarify the neural mechanisms underlying effort-related valuation and may provide candidate intervention targets for patients with decreased motivation to exert effort to obtain rewards.

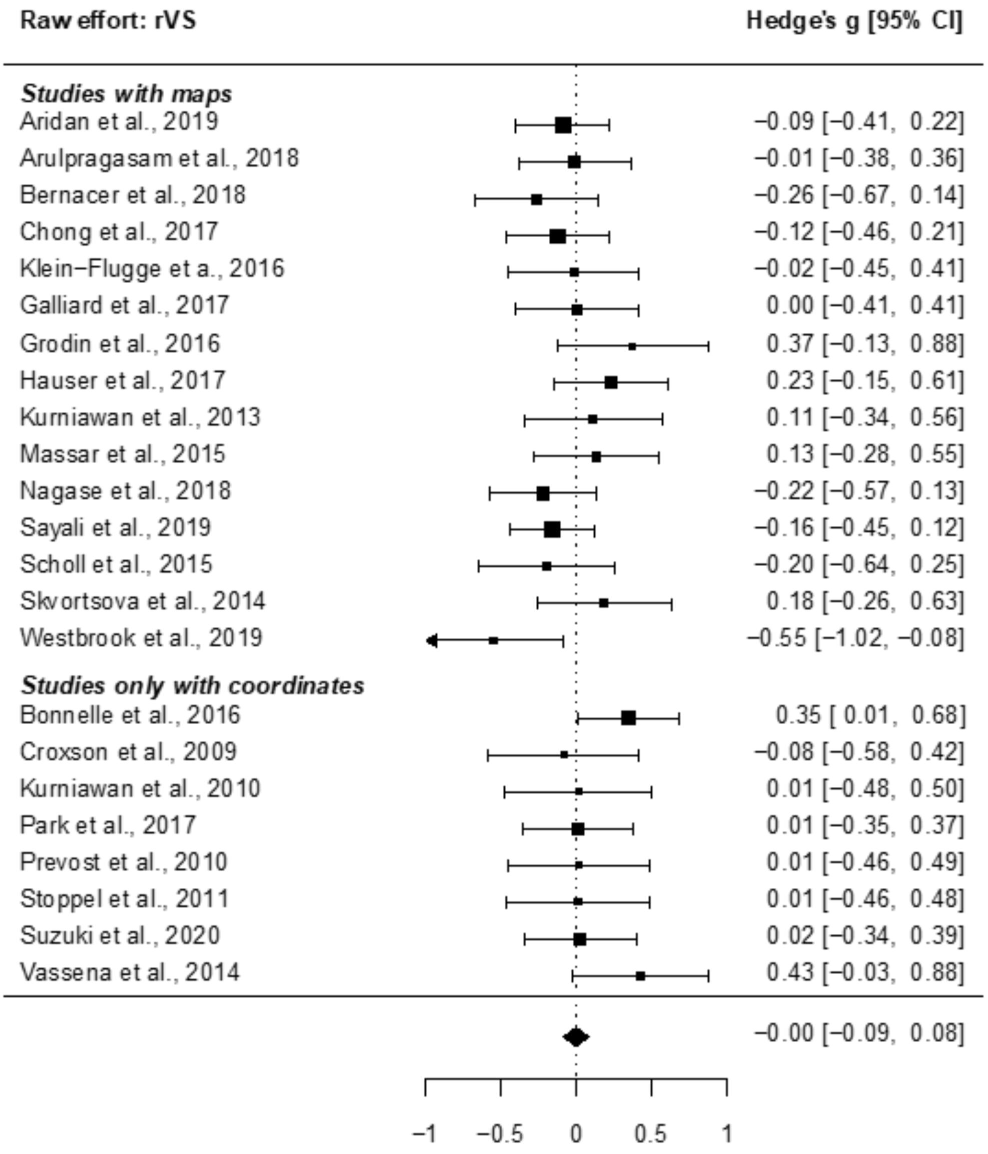


Figure 3.S1: Forest plot illustrating results of the raw effort analysis in the right VS ROI.

3.6 Supplementary Materials

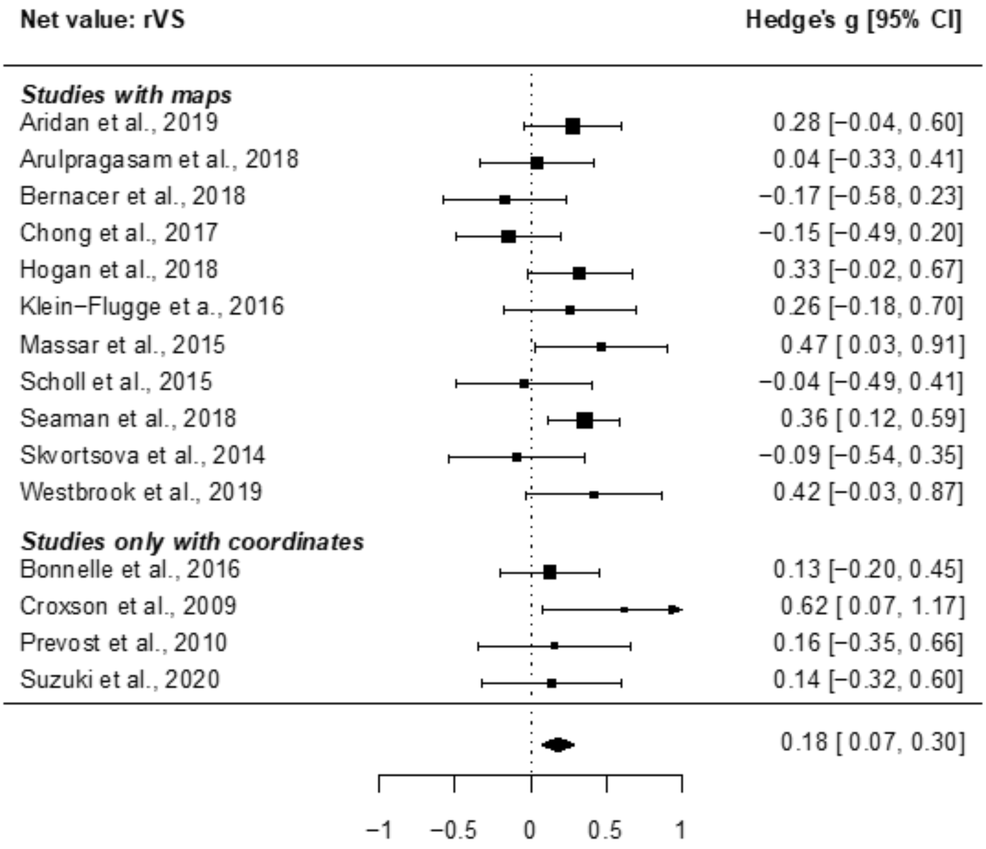


Figure 3.S2: Forest plot illustrating results of the net value analysis in the right VS ROI.

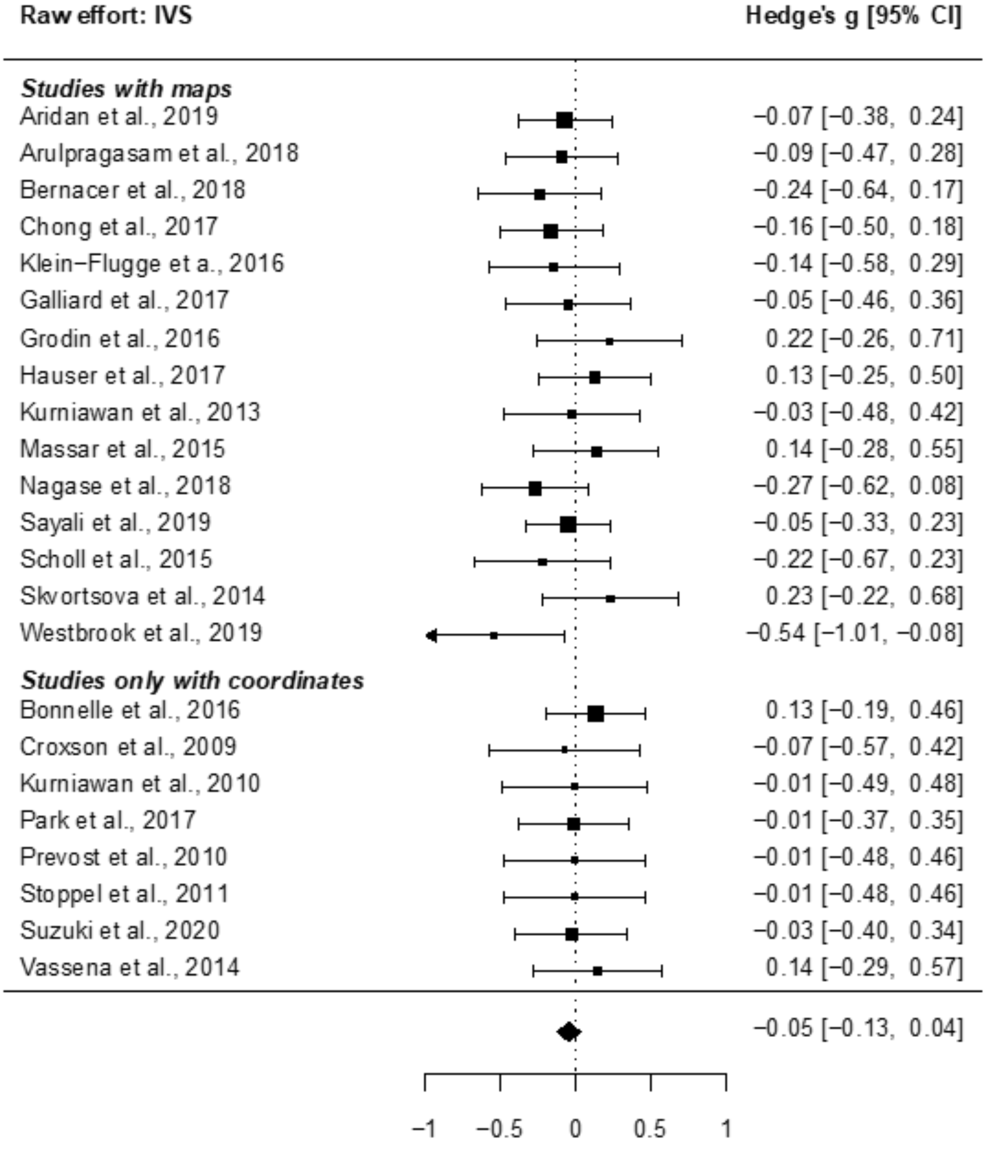


Figure 3.S3: Forest plot illustrating results of the raw effort analysis in the left VS ROI.

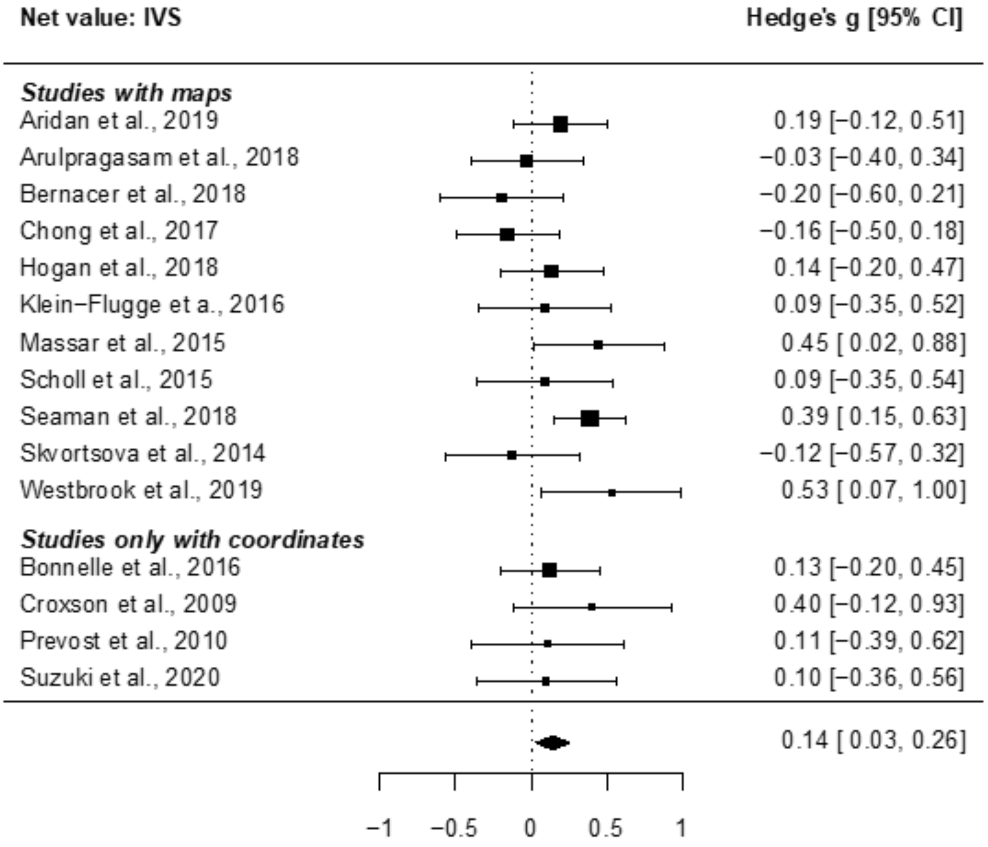


Figure 3.S4: Forest plot illustrating results of the net value analysis in the left VS ROI.

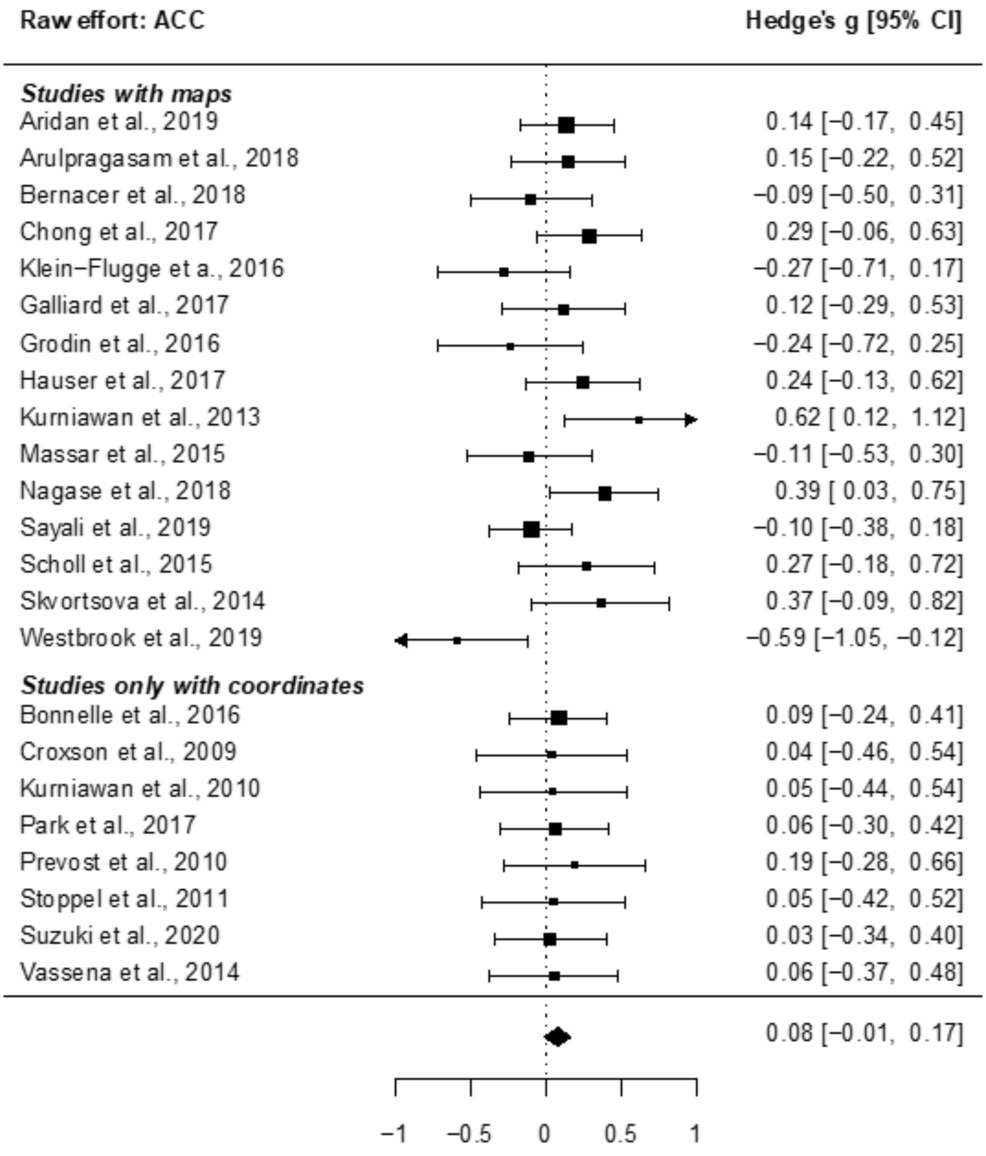


Figure 3.S5: Forest plot illustrating results of the raw effort analysis in the ACC ROI.

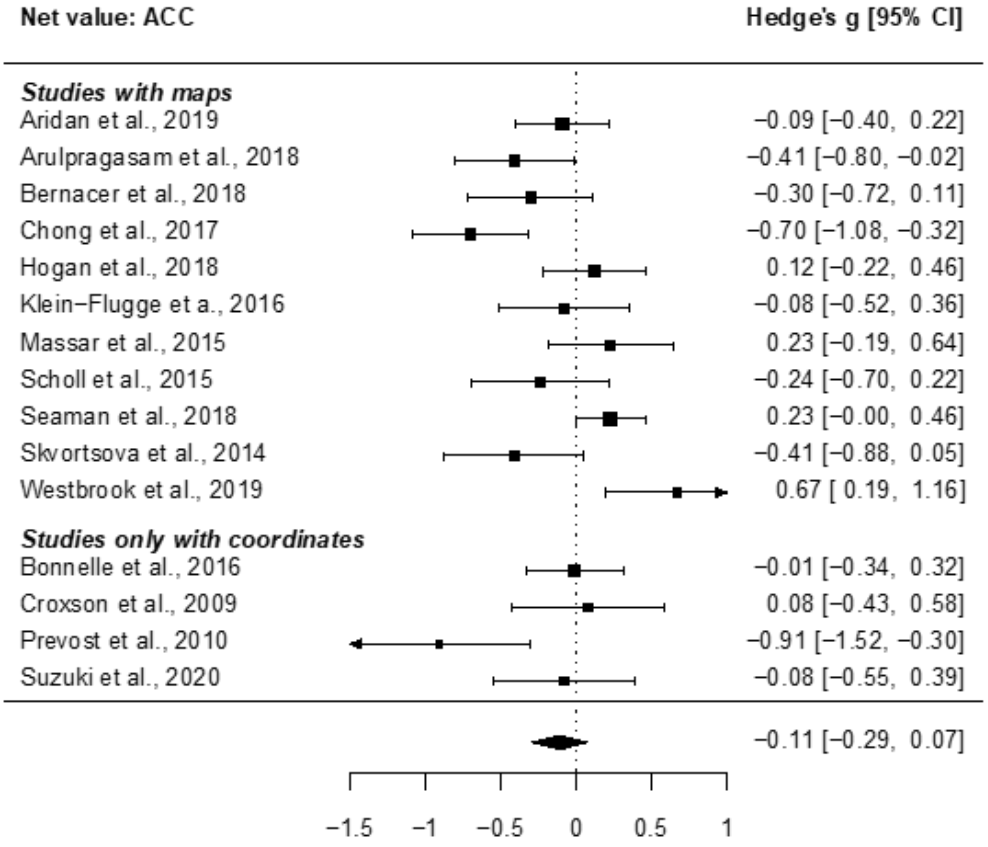


Figure 3.S6: Forest plot illustrating results of the net value analysis in the ACC ROI.

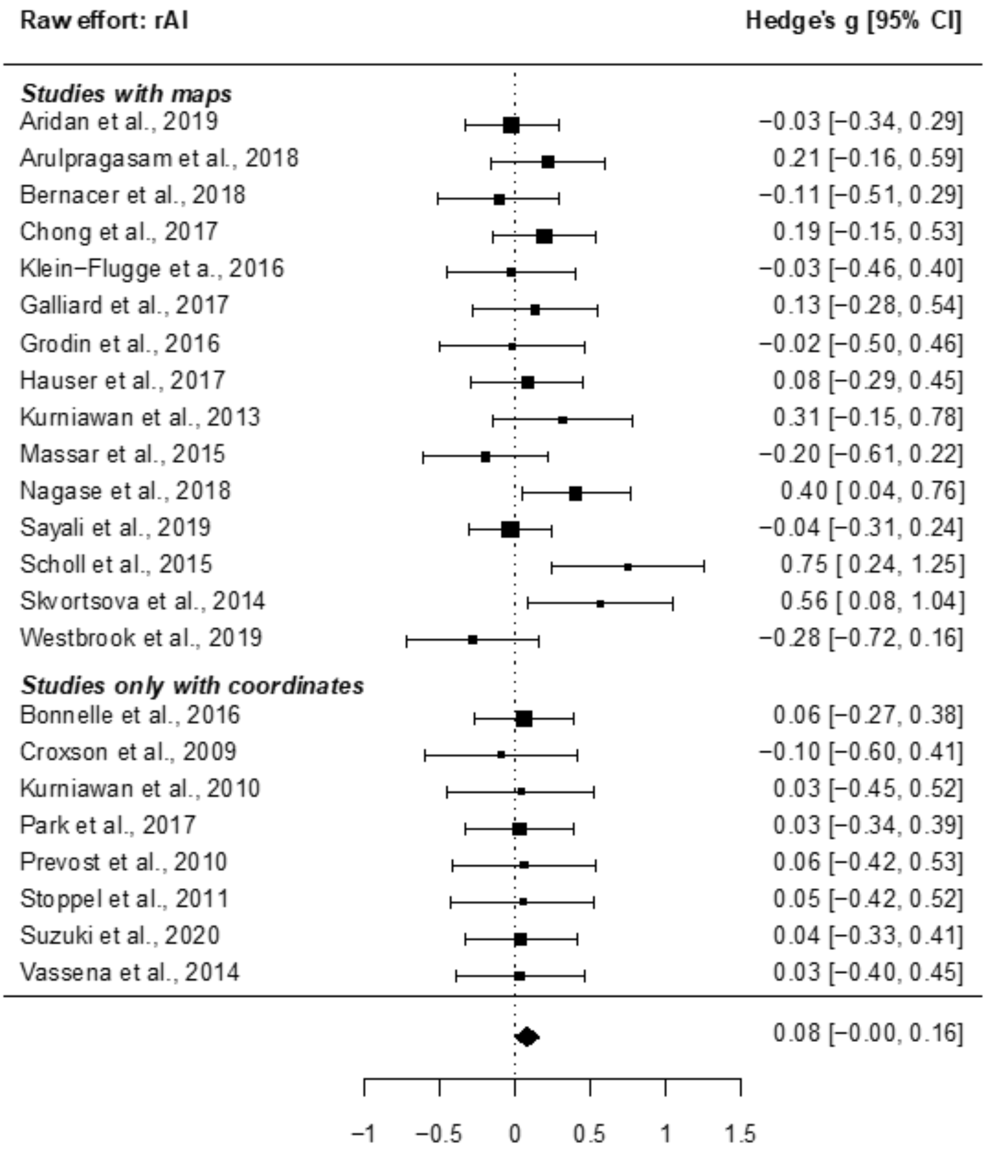


Figure 3.S7: Forest plot illustrating results of the raw effort analysis in the right AI ROI.

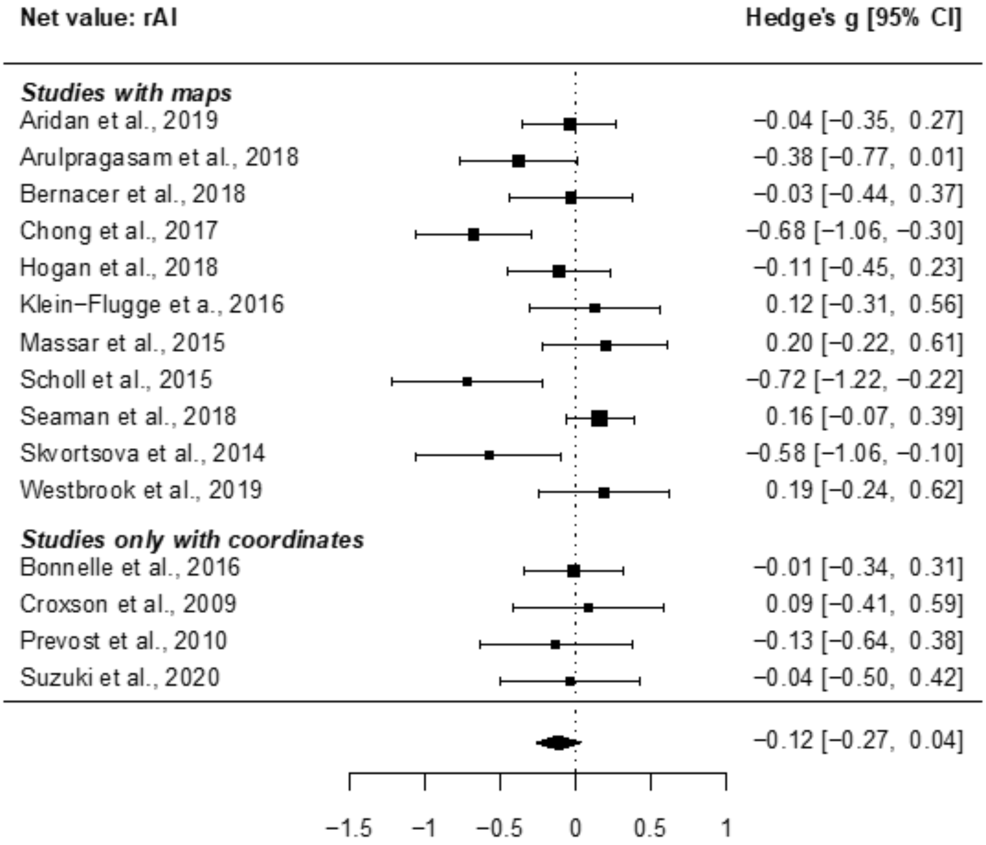


Figure 3.S8: Forest plot illustrating results of the net value analysis in the right AI ROI.

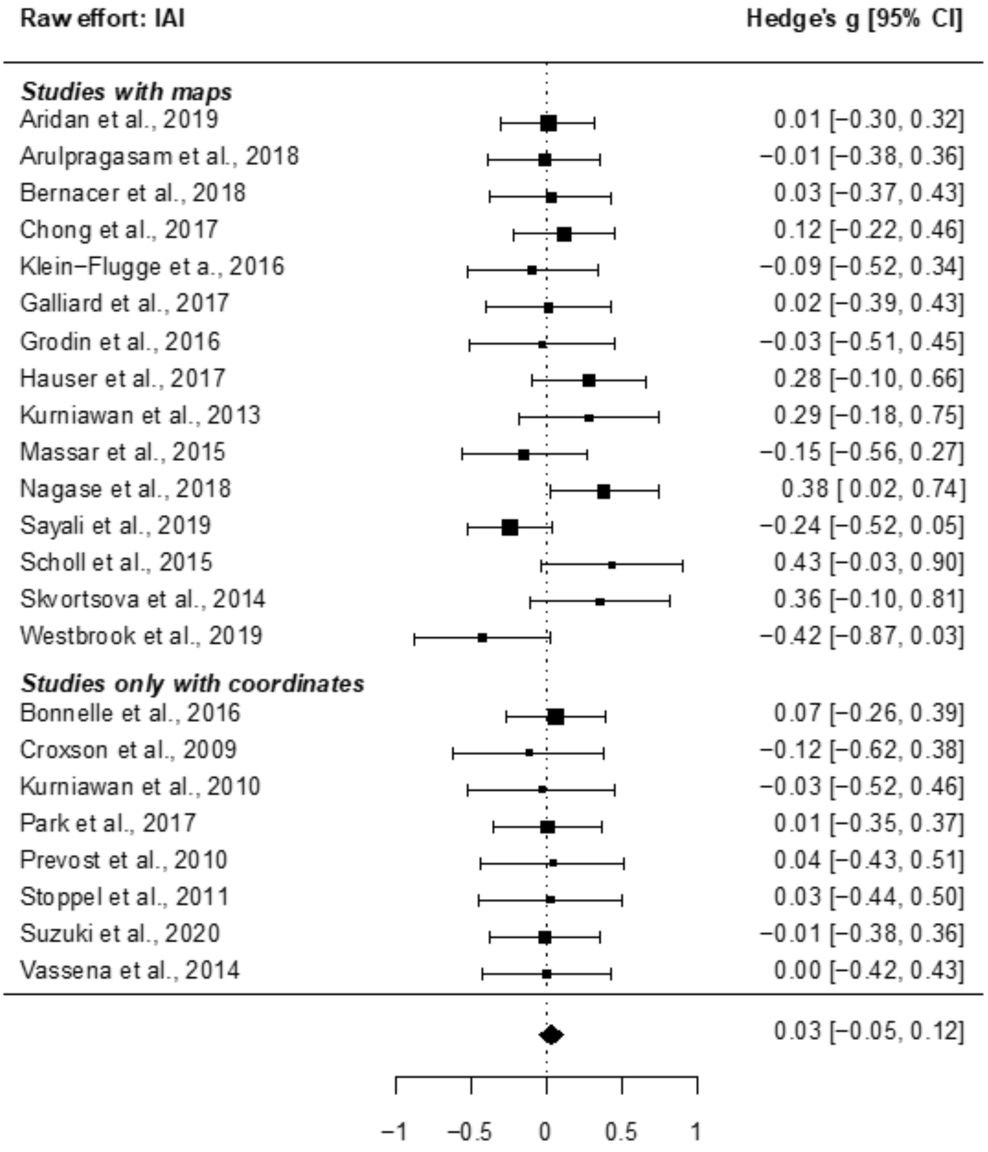


Figure 3.S9: Forest plot illustrating results of the raw effort analysis in the left AI ROI.

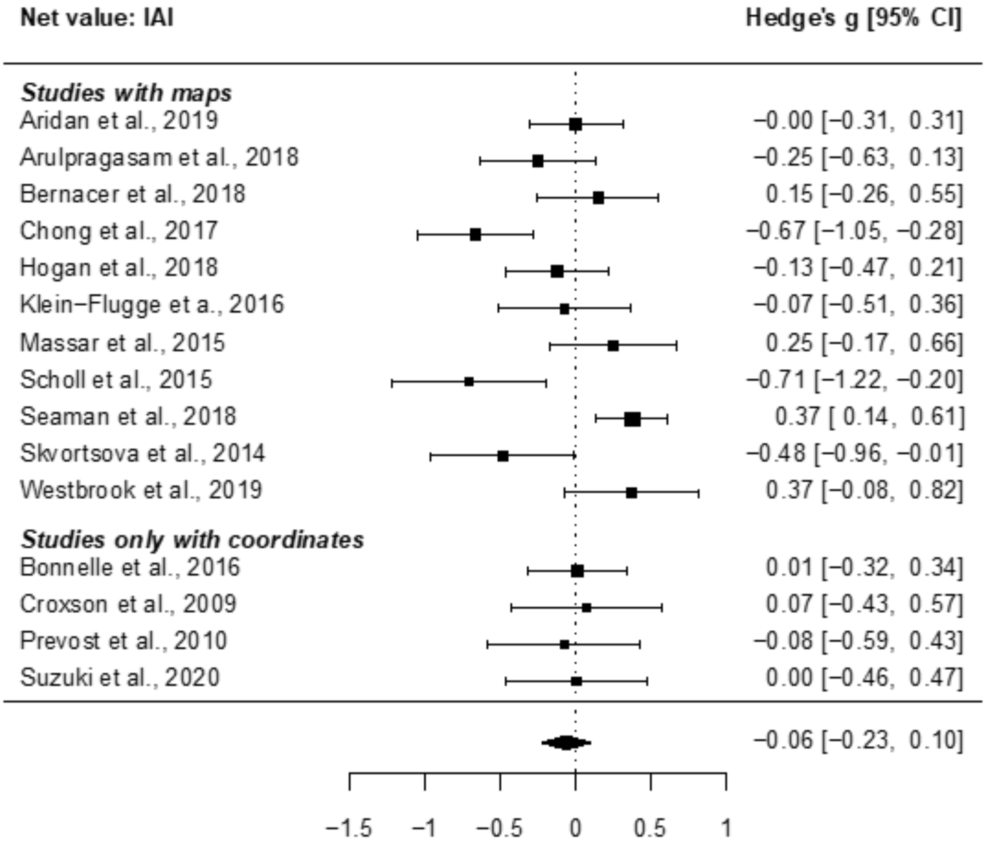


Figure 3.S10: Forest plot illustrating results of the net value analysis in the left AI ROI

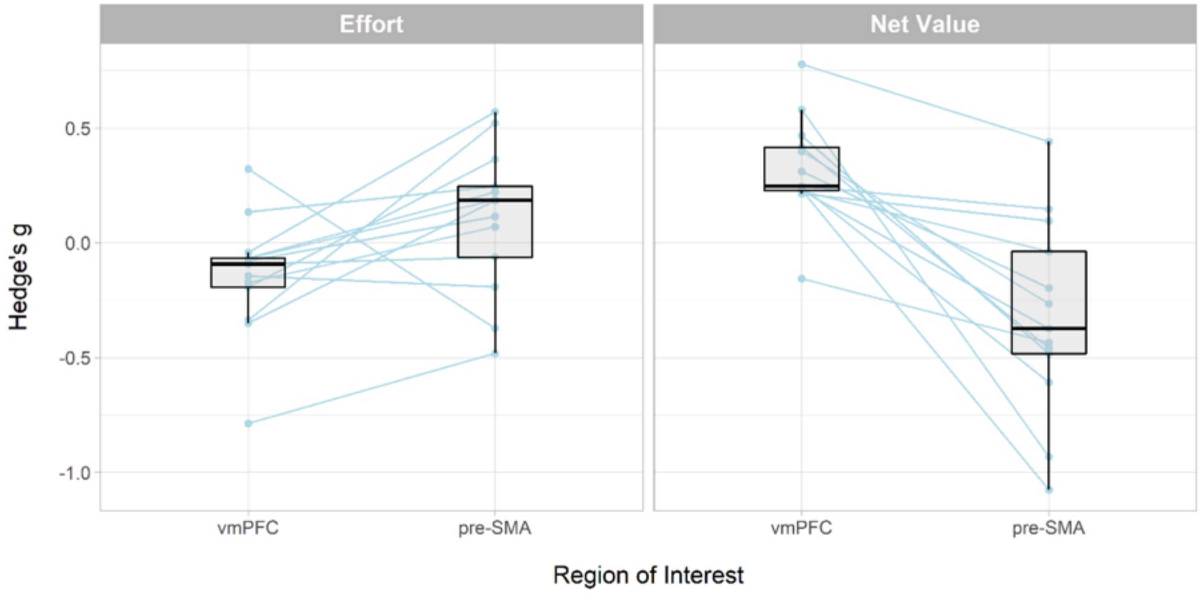


Figure 3.S11: Opposite activity patterns in the vmPFC and pre-SMA ROIs for effort and net value contrasts included in the linear mixed model (N=13). Light blue points correspond to the Hedge's *g* effect sizes of each study; light blue lines indicate that effect size values come from the same dataset. Box plots represent the median effect size and distribution of the data and are for illustrative purposes only. Please see Figures 2 and 3 for accurate estimates of 95% confidence intervals for effect sizes.

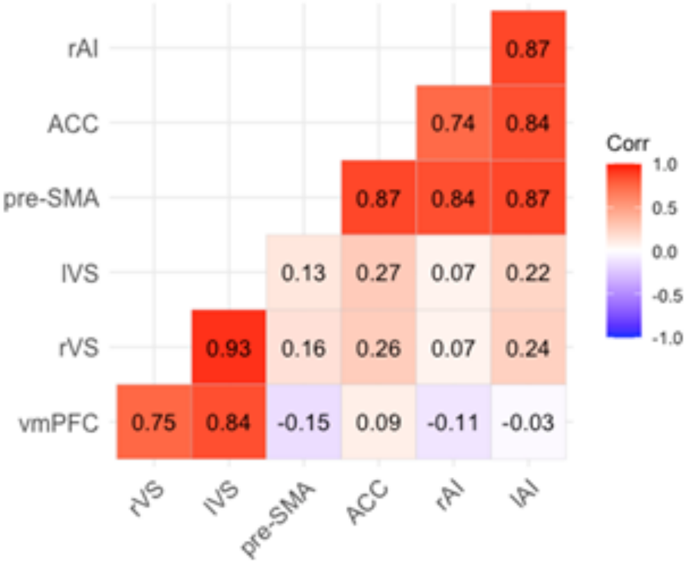


Figure 3.S12: Study-level correlation map for raw effort. The vmPFC and bilateral VS effect sizes were highly correlated across studies. Another network included the pre-SMA, ACC and bilateral AI.

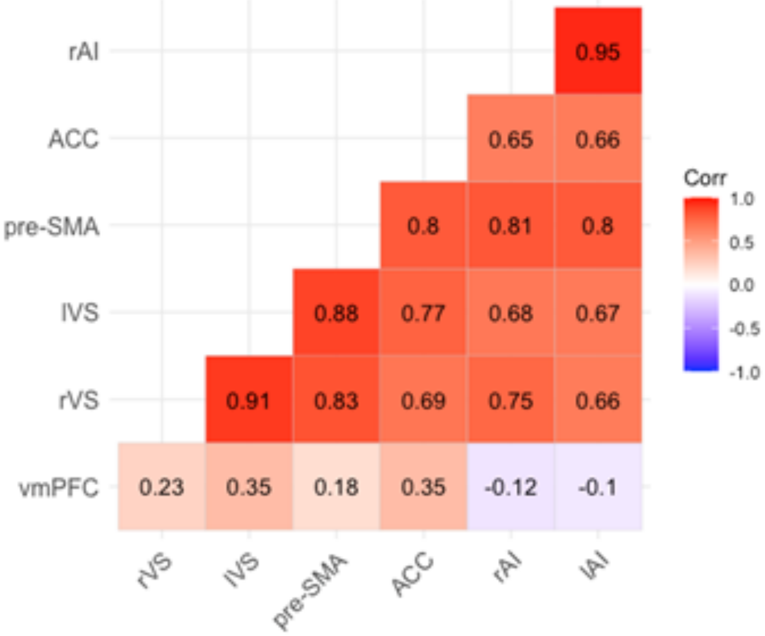


Figure 3.S13: Study-level correlation map for net value. The vmPFC appeared to be relatively independent. Other regions showed high correlations across studies.

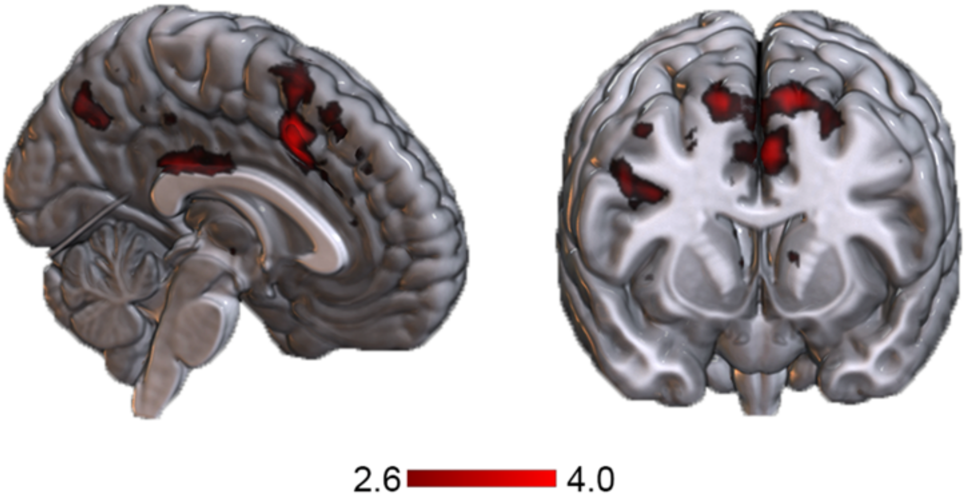


Figure 3.S14: Whole-brain meta-analytic results of physical effort subgroup analysis. Results use an uncorrected p<0.001 threshold and represent neural activity consistently related to prospective physical effort demands (N=16). Findings generally replicate activation activity in the supplementary motor area, as identified in the main effort meta-analysis. In addition, physical effort demands scale positively with activity in the bilateral precuneus, supramarginal gyrus, and posterior cingulate cortex. Unlike the main effort meta-analysis, physical effort did not scale negatively with any regions.

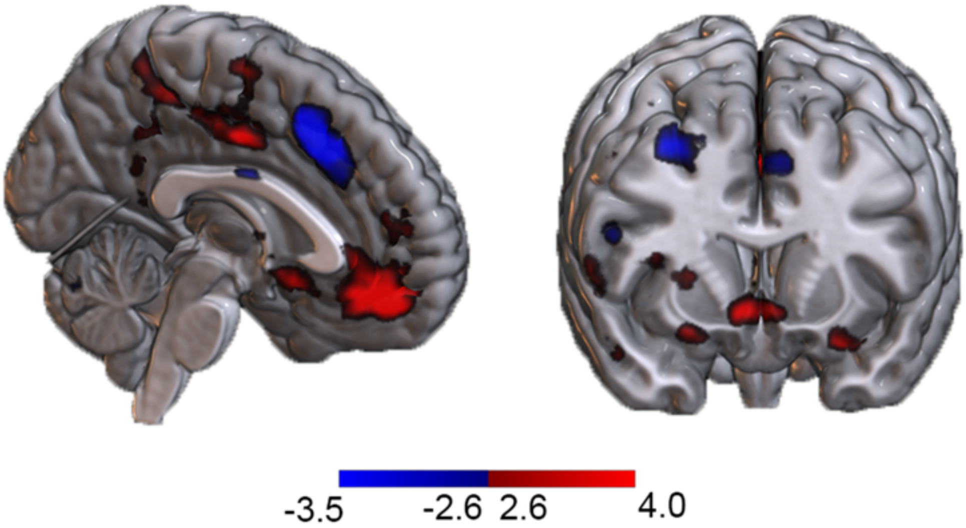


Figure 3.S15: Whole-brain meta-analytic results of net value analysis based on studies measuring physical effort (N=13). Results use an uncorrected p<0.001 threshold and represent neural activity consistently related to the net value of rewards with physical effort requirements. Findings generally replicate results of the main net value meta-analysis. Specifically, activity in the vmPFC, subgenual ACC, and PCC scaled positively and activity in the dACC/pre-SMA scaled negatively with higher net value of rewards with physical effort requirements.

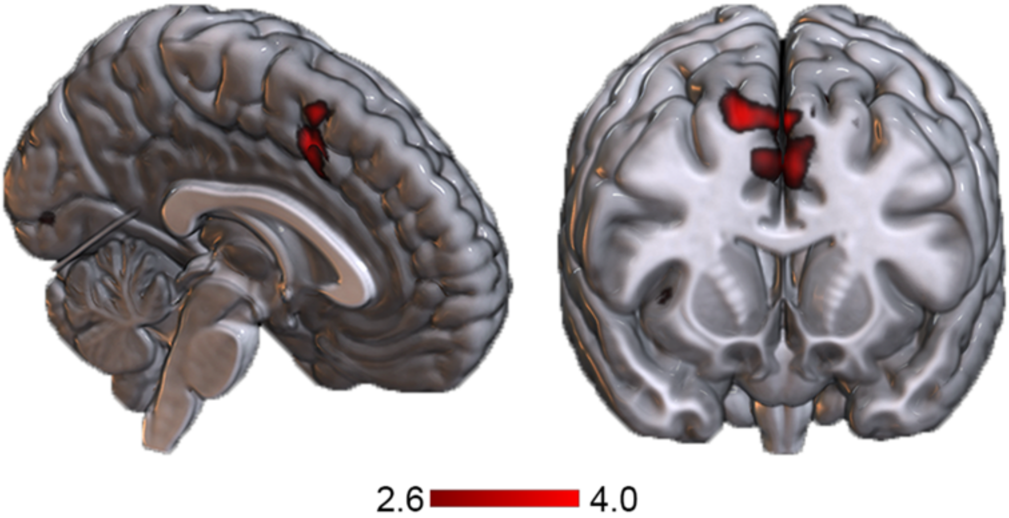


Figure 3.S16: Whole-brain meta-analytic results of raw effort analysis based on studies requiring effort execution during the task (N=16). Results use an uncorrected p<0.001 threshold and represent neural activity consistently related to prospective effort when immediate execution of effort requirements are required. Findings generally replicate results of the main raw effort meta-analysis; specifically, the cluster in the dACC/pre-SMA overlaps with a similar cluster identified in the main raw effort analysis.

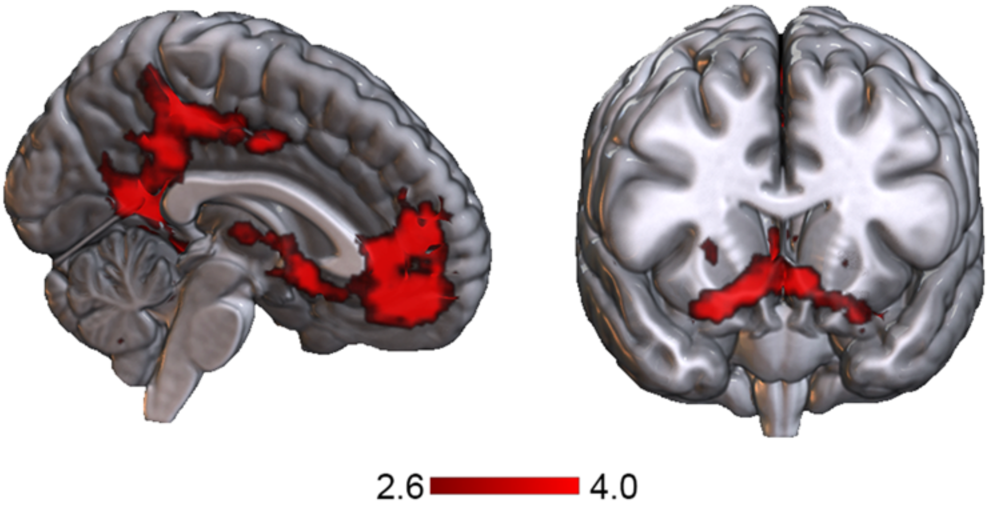


Figure 3.S17: Whole-brain meta-analytic results of single option net value subgroup analysis. Results use an uncorrected p<0.001 threshold and represent neural activity consistently related to effort-reward integration in studies using parameters that only include the net value of one choice option (N=11). Findings generally replicate activation activity in the main net value meta-analysis but did not detect any consistent deactivations.

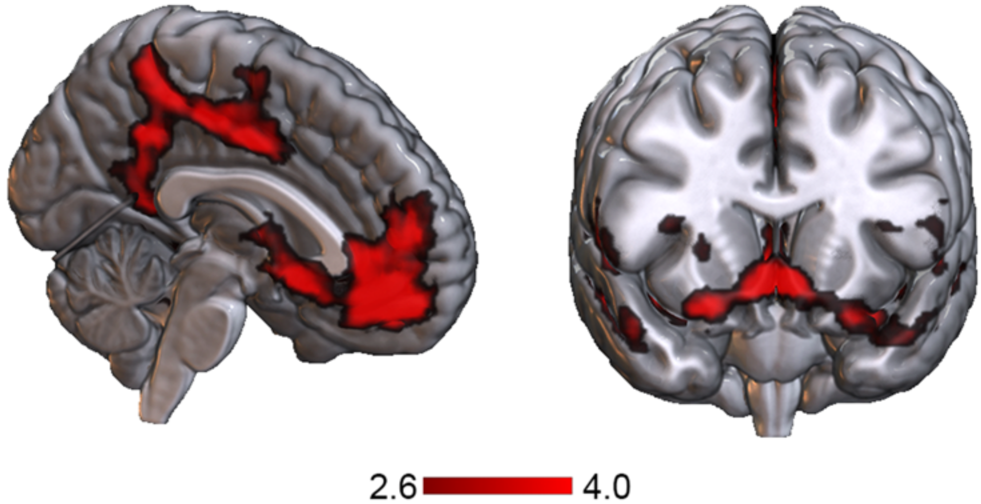


Figure 3.S18: Whole-brain meta-analytic results of net value supplementary analysis including studies with EffortXReward interaction parameters (N=17). Results use an uncorrected p<0.001 threshold. Findings generally replicate activation activity in the main net value meta-analysis but did not detect any consistent deactivations.

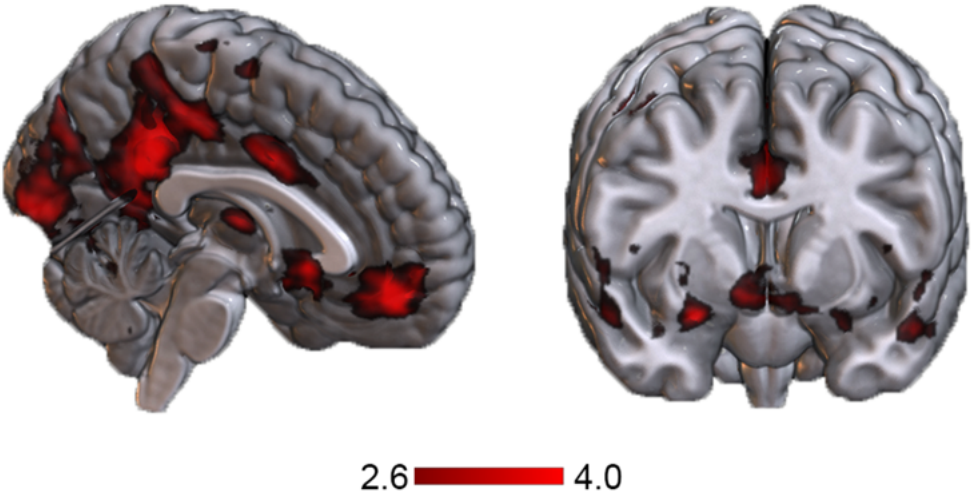
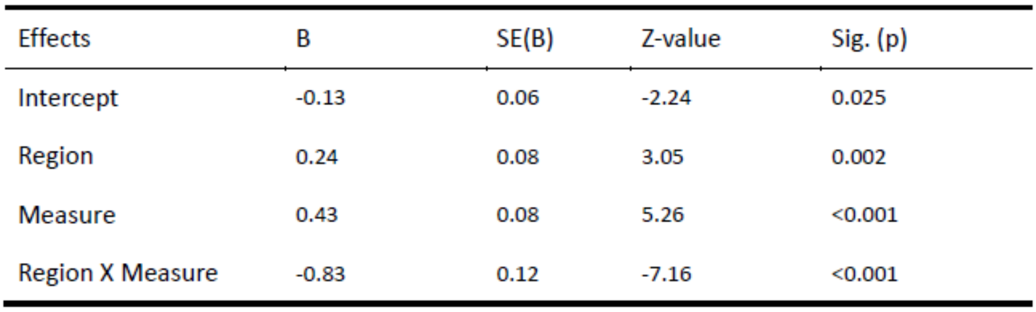


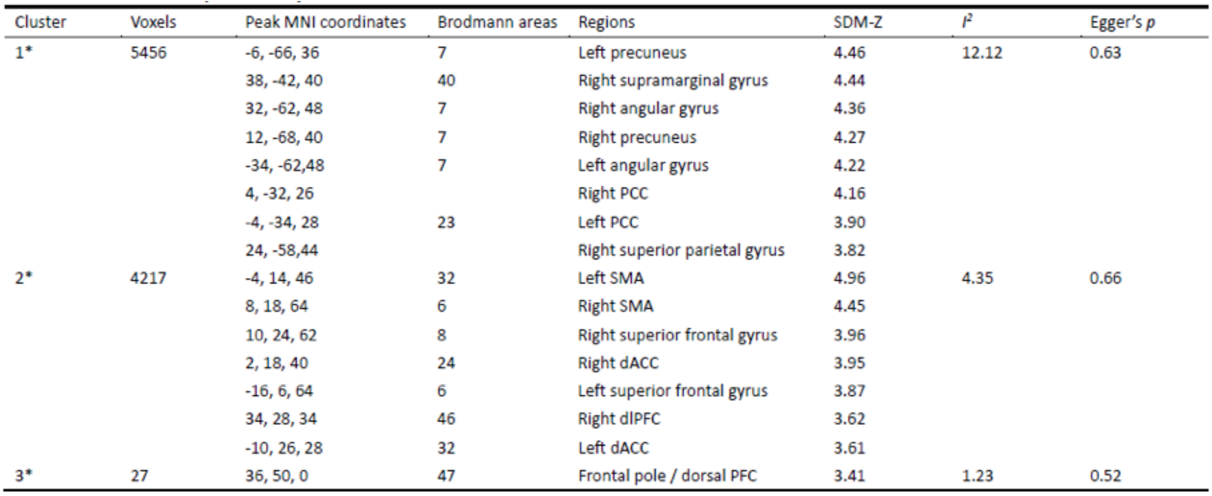
Figure 3.S19: Whole-brain meta-analytic results of raw reward analysis based on studies that tested reward processing (N=13). An uncorrected $p<0.001$ threshold is used for the display. The activity of a large neural network, including the vmPFC, VS, PCC, and some occipital regions, is positively associated with the reward magnitude.

3.7 Supplementary Tables



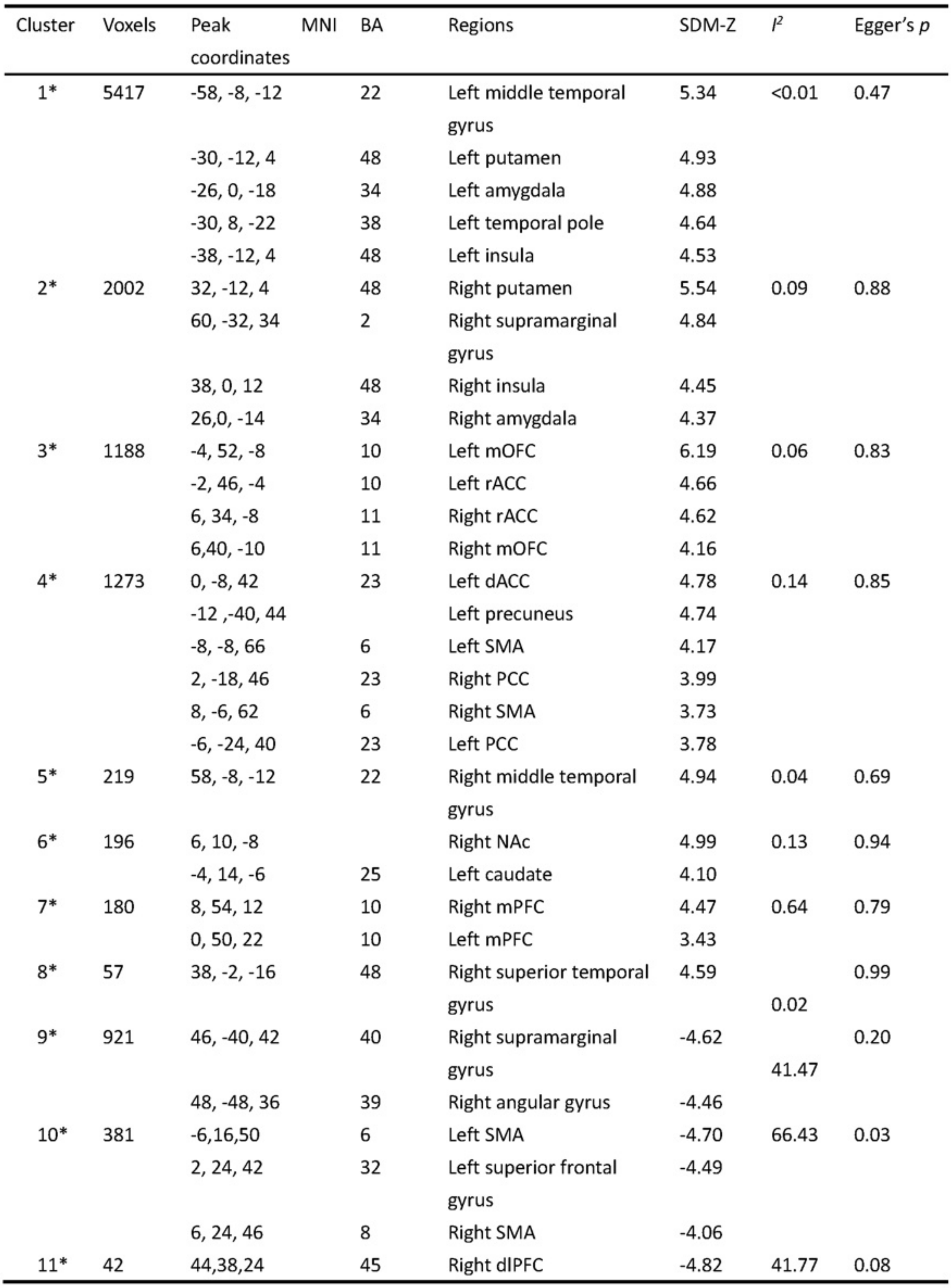
Effects	B	SE(B)	Z-value	Sig. (p)
Intercept	-0.13	0.06	-2.24	0.025
Region	0.24	0.08	3.05	0.002
Measure	0.43	0.08	5.26	<0.001
Region X Measure	-0.83	0.12	-7.16	<0.001

Table 3.S1: Linear Mixed-Effects Model.



Cluster	Voxels	Peak MNI coordinates	Brodmann areas	Regions	SDM-Z	I^2	Egger's *p*
1*	5456	-6, -66, 36	7	Left precuneus	4.46	12.12	0.63
		38, -42, 40	40	Right supramarginal gyrus	4.44		
		32, -62, 48	7	Right angular gyrus	4.36		
		12, -68, 40	7	Right precuneus	4.27		
		-34, -62,48	7	Left angular gyrus	4.22		
		4, -32, 26		Right PCC	4.16		
		-4, -34, 28	23	Left PCC	3.90		
		24, -58,44		Right superior parietal gyrus	3.82		
2*	4217	-4, 14, 46	32	Left SMA	4.96	4.35	0.66
		8, 18, 64	6	Right SMA	4.45		
		10, 24, 62	8	Right superior frontal gyrus	3.96		
		2, 18, 40	24	Right dACC	3.95		
		-16, 6, 64	6	Left superior frontal gyrus	3.87		
		34, 28, 34	46	Right dlPFC	3.62		
		-10, 26, 28	32	Left dACC	3.61		
3*	27	36, 50, 0	47	Frontal pole / dorsal PFC	3.41	1.23	0.52

Table 3.S2: Effect of Prospective Physical Effort on BOLD. Note: Data from 16 studies, using 8 parametric and 8 categorical parameters of prospective effort, were included in this analysis. Note that data from the physical effort task from Chong et al. (2017) was included in this analysis as well. All results survived a statistical threshold of voxel-level uncorrected p <0.001 and cluster size >20.
*Findings are FWER-corrected with a TFCE threshold of p <0.025.
Abbreviations: d, dorsal; SMA, supplementary motor area.

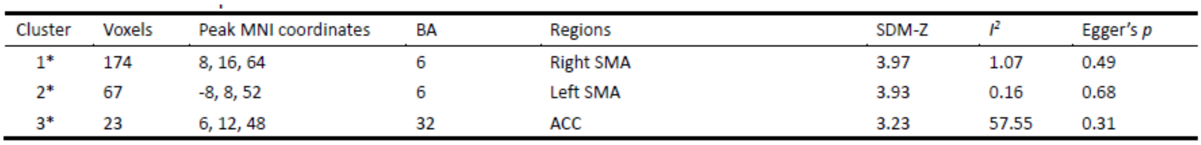


Cluster	Voxels	Peak MNI coordinates	BA	Regions	SDM-Z	I^2	Egger's *p*
1*	5417	-58, -8, -12	22	Left middle temporal gyrus	5.34	<0.01	0.47
		-30, -12, 4	48	Left putamen	4.93		
		-26, 0, -18	34	Left amygdala	4.88		
		-30, 8, -22	38	Left temporal pole	4.64		
		-38, -12, 4	48	Left insula	4.53		
2*	2002	32, -12, 4	48	Right putamen	5.54	0.09	0.88
		60, -32, 34	2	Right supramarginal gyrus	4.84		
		38, 0, 12	48	Right insula	4.45		
		26,0, -14	34	Right amygdala	4.37		
3*	1188	-4, 52, -8	10	Left mOFC	6.19	0.06	0.83
		-2, 46, -4	10	Left rACC	4.66		
		6, 34, -8	11	Right rACC	4.62		
		6,40, -10	11	Right mOFC	4.16		
4*	1273	0, -8, 42	23	Left dACC	4.78	0.14	0.85
		-12 ,-40, 44		Left precuneus	4.74		
		-8, -8, 66	6	Left SMA	4.17		
		2, -18, 46	23	Right PCC	3.99		
		8, -6, 62	6	Right SMA	3.73		
		-6, -24, 40	23	Left PCC	3.78		
5*	219	58, -8, -12	22	Right middle temporal gyrus	4.94	0.04	0.69
6*	196	6, 10, -8		Right NAc	4.99	0.13	0.94
		-4, 14, -6	25	Left caudate	4.10		
7*	180	8, 54, 12	10	Right mPFC	4.47	0.64	0.79
		0, 50, 22	10	Left mPFC	3.43		
8*	57	38, -2, -16	48	Right superior temporal gyrus	4.59	0.02	0.99
9*	921	46, -40, 42	40	Right supramarginal gyrus	-4.62	41.47	0.20
		48, -48, 36	39	Right angular gyrus	-4.46		
10*	381	-6,16,50	6	Left SMA	-4.70	66.43	0.03
		2, 24, 42	32	Left superior frontal gyrus	-4.49		
		6, 24, 46	8	Right SMA	-4.06		
11*	42	44,38,24	45	Right dlPFC	-4.82	41.77	0.08

Table 3.S3: Effect of Net Value of Rewards with Physical Effort Demands on BOLD. Note: Data from 13 studies, including the physical task from Chong, et al. (2017), from were included in this analysis. All results survived a statistical threshold of voxel-level uncorrected p <0.001 and cluster size >20.

*Regions survived FWER-correction with a TFCE threshold of p <0.025.

Abbreviations: BA, Brodmann areas; m, medial; dl, dorsolateral; r, rostral; PFC, prefrontal cortex; OFC, orbitofrontral cortex; NAc, neural accumbens; ACC, anterior cingulate cortex; SMA, sensory motor area.

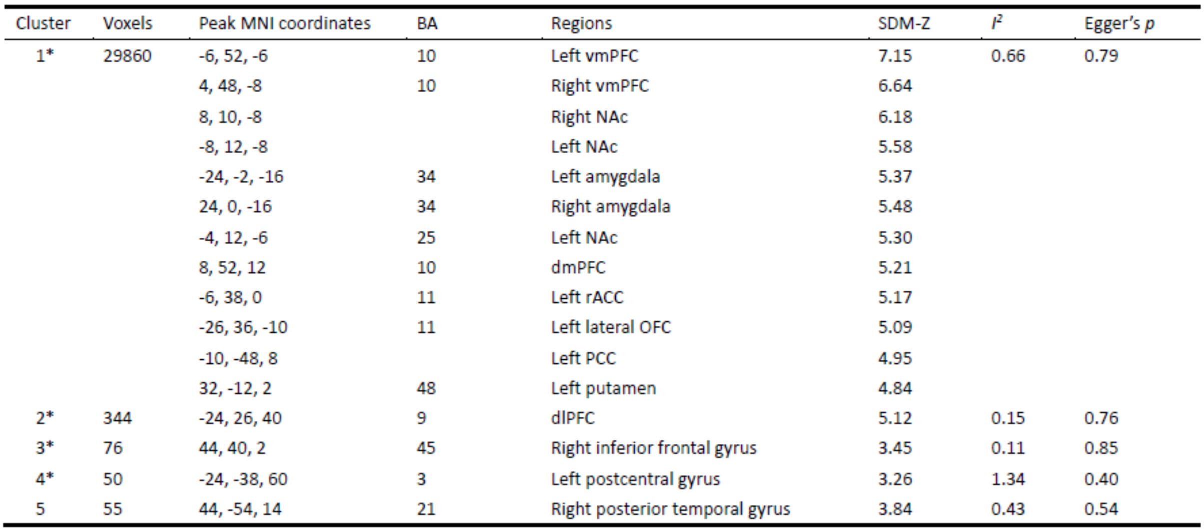


Cluster	Voxels	Peak MNI coordinates	BA	Regions	SDM-Z	I^2	Egger's *p*
1*	174	8, 16, 64	6	Right SMA	3.97	1.07	0.49
2*	67	-8, 8, 52	6	Left SMA	3.93	0.16	0.68
3*	23	6, 12, 48	32	ACC	3.23	57.55	0.31

Table 3.S4: Effect of Prospective Effort with Online Effort Execution on BOLD. Note: Data from 15 studies were included in this analysis. All results survived a statistical threshold of voxel-level uncorrected p <0.001 and cluster size >20.

[*] Regions survived FWER-correction with a TFCE threshold of p <0.025.

Abbreviations: BA, Brodmann areas; ACC, anterior cingulate cortex; SMA, sensory motor area.



Cluster	Voxels	Peak MNI coordinates	BA	Regions	SDM-Z	I^2	Egger's *p*
1*	29860	-6, 52, -6	10	Left vmPFC	7.15	0.66	0.79
		4, 48, -8	10	Right vmPFC	6.64		
		8, 10, -8		Right NAc	6.18		
		-8, 12, -8		Left NAc	5.58		
		-24, -2, -16	34	Left amygdala	5.37		
		24, 0, -16	34	Right amygdala	5.48		
		-4, 12, -6	25	Left NAc	5.30		
		8, 52, 12	10	dmPFC	5.21		
		-6, 38, 0	11	Left rACC	5.17		
		-26, 36, -10	11	Left lateral OFC	5.09		
		-10, -48, 8		Left PCC	4.95		
		32, -12, 2	48	Left putamen	4.84		
2*	344	-24, 26, 40	9	dlPFC	5.12	0.15	0.76
3*	76	44, 40, 2	45	Right inferior frontal gyrus	3.45	0.11	0.85
4*	50	-24, -38, 60	3	Left postcentral gyrus	3.26	1.34	0.40
5	55	44, -54, 14	21	Right posterior temporal gyrus	3.84	0.43	0.54

Table 3.S5: Effect of One-Parameter Net Value on BOLD. Note: Data from 11 studies were included in this analysis. All results survived a statistical threshold of voxel-level uncorrected p <0.001 and cluster size >20.

[*] Regions survived FWER-correction with a TFCE threshold of p <0.025.

Abbreviations: BA, Brodmann areas; vm, ventromedial; dm, dorsomedial; dl, dorsolateral; r, rostral; PFC, prefrontal cortex; NAc, neural accumbens; ACC, anterior cingulate cortex; PCC, posterior cingulate cortex; OFC, orbitofrontal cortex.

Cluster	Voxels	Peak MNI coordinates	BA	Regions	SDM-Z	I^2	Egger's *p*
1*	24611	-4, 52, -8	10	Left vmPFC	6.97	0.31	0.79
		2, 50, -8	10	Right vmPFC	6.63		
		8, 10, -8		Right NAc	6.48		
		32, -12, 4	48	Right putamen	5.81		
		-2, 40, -10	11	Left rACC	5.81		
		10, 50, 12	32	Right dmPFC	5.79		
		-6, 14, -8	25	Left caudate	5.17		
		24, 0, -16	34	Right amygdala	5.54		
		-22, -6, -14	34	Left amygdala	5.53		
		-32, -16, 4	48	Left insula	5.49		
		34, 34, 12	47	Left lateral OFC	4.93		
2*	4473	-14, -38, 40		Left PCC	5.55	5.05	0.51
		-12, -40, 44		Left precuneus	5.41		
		0, -8, 42	23	ACC	5.07		
		8, -34, 52		Right PCC	4.95		
3*	520	-26, 28, 38	9	Left dlPFC	4.20	2.89	0.62
4	130	44, 38, 24	45	Right inferior frontal gyrus	-4.17	48.18	0.26
5	126	-8, 16, 52	6	Left SMA	-3.61	62.46	0.13
6	26	16, 20, 58	8	Right dlPFC	-3.64	35.23	0.40

Table 3.S6: Effect of Net Value (with Effort X Reward interaction) on BOLD. Note: Data from 17 studies were included in this analysis. All results survived a statistical threshold of voxel-level uncorrected p <0.001 and cluster size >20.

* Regions survived FWER-correction with a TFCE threshold of p <0.025.

Abbreviations: BA, Brodmann areas; vm, ventromedial; dm, dorsomedial; dl, dorsolateral; r, rostral; PFC, prefrontal cortex; NAc, neural accumbens; ACC, anterior cingulate cortex; PCC, posterior cingulate cortex; SMA, sensory motor area.

Cluster	Voxels	Peak MNI coordinates	BA	Regions	SDM-Z	I^2	Egger's *p*
1*	53229	6,-92,2	17	Right cuneus	5.63	0.04	0.95
		-10, -40, 36	23	Left PCC	5.22		
		2, -44, 36	23	Right PCC	4.41		
		-8, 40, -8	11	Left vmPFC	5.33		
		10, 48, -10	10	Right vmPFC	5.14		
		8, 36, -8	11	Right rACC	4.93		
		-10, 12, -10		Left caudate	3.89		
		14, 26, -2		Right caudate	3.785		
		-48, -72, 24	39	Left angular gyrus	5.10		
		-32, -42, -24	37	Left fusiform gyrus	4.21		
		54, -34, 24		Right supramarginal gyrus	4.28		
		38, -24, 56	4	Right precentral gyrus	4.15		
		60, 06, 016	21	Right middle temporal gyrus	3.90		
		2, 2, 36	24	Right dACC	4.33		
		0, 8, 32		Left dACC	3.65		
		52, -50, 20	22	Right middle temporal gyrus	3.85		
		26, 4, -16	34	Right amygdala	4.33		
		-52, -2, -20	21	Left middle temporal gyrus	4.46		
		-60, -44, 26	48	Left supramarginal gyrus	3.67		
		-22, -4, -16	34	Left amygdala	4.06		
2*	131	0, -12, 10		Thalamus	4.14	<0.00	0.668

Table 3.S7: Effect of Reward on BOLD. Note: Data from 13 studies were included in this analysis. All results survived a statistical threshold of voxel-level uncorrected p <0.001 and cluster size >20.

* Regions survived FWER-correction with a TFCE threshold of p <0.025.

Abbreviations: BA, Brodmann areas; vm, ventromedial; r, rostral; d, dorsal; PCC, posterior cingulate cortex; ACC, anterior cingulate cortex.

Chapter 4

Disentangling Effort from Probability of Success: Theta Oscillatory Dynamics Reveal the Role of Medial Prefrontal Cortex in Effort-Based Reward[*]

4.1 Abstract

The ability to weigh a reward against the cost of acquiring it is critical for decision-making. While the medial prefrontal cortex (mPFC) has been implicated in tracking both mental effort demands and net value of rewards, these findings primarily come from choice paradigms that confound increased task difficulty with decreased reward probability. To resolve this issue, we designed novel tasks that kept probability of success – and therefore probability of reward – constant between levels of effort demand. In two experiments, participants completed a novel effort-based reward task that manipulated effort demand and either reward magnitude or probability of success. Electroencephalogram (EEG) data was recorded to compare an electrophysiological index of mPFC function (frontal midline theta (FMT)) to an index of incentive salience (component P3) at both cue evaluation and feedback phases. We found no evidence that FMT tracked effort demands or net value during cue evaluation. At feedback, however, FMT power was enhanced for high compared to low effort trials, but not modulated by reward magnitude or probability. Conversely, P3 was sensitive to reward magnitude and probability at both cue and feedback phases and only integrated expended effort costs at feedback, such that P3 amplitudes continued to scale with reward magnitude and probability but were also increased for high compared to low effort reward feedback. These findings suggest that, in the absence of option comparison and unequal likelihood of success, the mPFC does not track net value of prospective effort-based rewards. Instead, expended cognitive effort potentiates FMT power and enhances the saliency of rewards at feedback.

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[*] This study has been submitted to Cortex and is currently being reviewed.

4.2 Introduction

Overcoming effort costs to obtain a reward is critical for successful goal-directed behavior (Westbrook and Braver, 2015; Zald and Treadway, 2017). In the case of effort-based rewards, the medial prefrontal cortex (mPFC), including the pre-supplementary motor area and the dorsal anterior cingulate cortex (dACC), has emerged as a key neural hub in tracking net value (Arulpragasam et al., 2018; Chong et al., 2017; Croxson et al., 2009; Massar et al., 2015; Skvortsova et al., 2014) and upcoming effort costs (Chong et al., 2017; Klein-Flugge et al., 2016; Prévost et al., 2010; Vassena, Krebs, et al., 2014).

However, the functions of the mPFC are highly heterogeneous, making it difficult to determine if the mPFC is integrating effort with reward values or if it is responding to other task-related variables. Specifically, the mPFC has been linked to a variety of cognitive control functions that subserve value-based decision-making, such as prediction error signaling (Vassena et al., 2020; Vassena, Holroyd, et al., 2017), attention (Aarts and Roelofs, 2011; Aarts et al., 2008), conflict monitoring and response inhibition (Botvinick and Braver, 2015; Botvinick et al., 2001), invigoration (Kouneiher et al., 2009; Kurniawan et al., 2013), and option comparison (Hogan et al., 2019; Kolling et al., 2016; Shenhav et al., 2013; Shenhav et al., 2014; Westbrook et al., 2019). Furthermore, electrophysiological markers of mPFC functioning are sensitive to reward probability and uncertainty (Bellebaum et al., 2010; B. W. Smith et al., 2009; Yu et al., 2011). This is critical, as several studies have reported poorer performance for high, compared to low, effort tasks (Aridan et al., 2019; Giustiniani et al., 2020; Grodin et al., 2016; Ma et al., 2014; Umemoto et al., 2022; Wang et al., 2017; Yi et al., 2020), potentially confounding increased effort demand with reduced reward likelihood. Thus, to adequately investigate the role of the mPFC in tracking effort-based rewards, experimental paradigms must be able to manipulate effort demand while simultaneously ensuring that increases in difficulty are not associated with reduced reward probability.

To this aim, we designed two novel paradigms that rewarded participants based on task performance but yielded similar reward rates for low and high levels of effort demand. Specifically, we investigated to what degree manipulations in effort demand, reward magnitude (Study 1), and reward probability (Study 2) modulate activity in the mPFC – putatively measured by frontal midline theta (FMT) – at both cue evaluation and feedback processing phases. FMT is an EEG oscillatory activity of 4-8 Hz that is distributed over fronto-central areas of the scalp and has been linked to a range of cognitive control (Cavanagh and Frank, 2014; Cavanagh and Shackman, 2015) and performance feedback functions (Doñamayor et al., 2012; Li et al., 2016; Li et al., 2018; Mas-Herrero and Marco-Pallarés, 2014, 2016). Generated in the mPFC (Mas-Herrero and Marco-Pallarés, 2016), FMT has been hypothesized to reflect effortful control in goal-directed behavior (Cavanagh and Frank, 2014; Holroyd and Umemoto, 2016), improve behavioral performance via phase-amplitude coupling (Verguts, 2017), track task-relevant features (Hajihosseini and Holroyd, 2013), and correlate with trial-by-trial behavioral adjustments (Cavanagh and Shackman, 2015). Taken together, FMT is a candidate EEG signature for the allocation of control in effort-based reward. We hypothesized that if the mPFC tracks the motivational value of effort-based rewards, FMT activity would reflect an integrated effort and reward signal at both cue and feedback. In parallel, due to the novelty of the task, we tested the effectiveness of our manipulations using an established index of incentive salience – the P3 event-related potential (ERP; Glazer et al., 2018). Several studies have shown that P3 amplitudes are modulated by reward magnitude and probability at cue and feedback (Giustiniani et al., 2020; Hajcak et al., 2005; Hajcak et al., 2007; Pfabigan et al., 2014; Vignapiano et al., 2016), as well as previously expended effort at reward feedback (Ma et al., 2014; Schevernels et al., 2014; Wang et al., 2017). Thus, if our manipulations were effective, we expected P3 to be sensitive to these reward features as well.

4.3 Methods

4.3.1 Study 1

4.3.1.1 Participants

Sensitivity analyses indicated that a sample size of N=27 would provide 80% statistical power to detect effect sizes of η_p^2= 0.06 or larger. Subjects were excluded for current psychiatric diagnosis, color blindness, and lack of fluency in Spanish. 33 healthy adults (20 female, age: M= 27.24, SD=5.45) participated in the study. One subject was removed for low cue identification rate (<50%) in the catch questions and three subjects were removed for excessive motion artifacts, leaving a final sample of N=28.

4.3.1.2 Procedures

Upon arrival, participants reviewed and provided informed consent. Next, participants completed a series of self-report demographic and COVID-19 health questionnaires and then the Effort Valuation Task (see below). After the task, participants completed an end of session questionnaire (described below) before debriefing. All participants received a baseline payment of 20€ for participation, and additional earnings from the Effort Valuation Task, ranging from 5€ to 15€. This study was conducted in accordance with the ethical guidelines from the Declaration of Helsinki and was approved by the University of Barcelona ethics board.

Effort Valuation Task. The current Effort Valuation Task comprised of a variant of the reward effortful task used in Croxson et al. (2009), modified to use an effort component from Botvinick et al. (2009). The task was administered using PsychoPy software version 2 (Peirce et al., 2019). Subjects were seated approximately 50 cm away from the computer monitor and responded using a standard keyboard and mouse. The schematic of the task is shown in Figure 4.1a. First, a cue signaling the prospective effort and reward of the upcoming trial was presented for 1.5 seconds. The shape of the cue (circle or square, counterbalanced across participants) indicated the effort requirement (low vs high) and the number of lines indicated the magnitude of reward on offer, with 1 line indicating low reward (5 points) and 5 lines indicating high reward (25 points).

Half of trials were work trials, while the other half were no-work trials. In effort trials, cues were followed by a fixation cross (randomized time of presentation between 1200 and 1500 ms, with 100 ms steps) and then an effort phase, which lasted 8 seconds. During the effort phase, subjects viewed a series of numbers presented one at a time on the screen. Numbers ranged from one to nine, excluding five. If the number was blue, subjects were instructed to use the arrow keys to indicate if the number was even or odd. If the number was yellow, subjects were instructed to indicate whether the number was higher or lower than 5. In low effort trials, all judgments were of the same type. In the high effort trials, number color/judgment type alternated, requiring effortful cognitive set switches (Botvinick, 2007; Lopez-Gamundi and Wardle, 2018). Participants were instructed to answer as quickly and as accurately as possible within the 8-second time frame. Immediately after the effort phase, another fixation cross appeared for 2000 to 2500 ms (steps of 100 ms), followed by a reward/performance feedback for 1000 ms. If participants correctly completed the task, a 5 or 25 was presented on the screen, matching the reward offer for the trial. If participants made more than 2 errors during the task or did not meet the calibrated decision threshold (see Training and Calibration for more detail), an X was presented indicating that the trial was not successful, and no points were being awarded. Another fixation cross marked the end of the trial. Intertrial intervals (ITIs) ranged from 2 to 3 seconds (with steps of 200 ms).

Conversely, no-work trials started with the same joint reward-effort cues but, instead, were followed by an asterisk (1200 - 1500 ms, with 100 ms steps), indicating no work was required and that no points would be awarded for that trial. To ensure that participants attended to the reward/effort cue, four no-work trials in each block were followed by an identification question. Participants had to use the keypad to recall the meaning of the cue that had been presented at the beginning of the trial; for example, if the cue was a circle with 1 line in it, the participant had to select the option that read “easy task worth 5 points”. Participants were instructed that compensation depended partially on how accurate they answered these identification questions. Identification questions were self-paced and no feedback was provided until the break screen. No-work trials ended with the same fixation cross and ITI.

There were five blocks with 80 trials (40 work, 36 no-work, and 4 no-work followed by an identification question) per block, totaling to 400 trials. Reward and effort conditions were intermixed and evenly distributed between work/no-work trials, so that in each block there were 10 work trials and 10 no-work trials for each of the 4 following cues: high reward/high effort, high reward/low effort, low reward/high effort and low reward/low effort. Trials were presented in pseudo-random order, such that there were no more than 2 consecutive no-effort trials. Participants were probed for fatigue, cue liking, and task difficulty (see Self-Report) after calibration, as well as halfway through and at the end of each block, making for 11 ratings total. After these questions, participants were given a self-paced break and provided with feedback about their cumulative points and their identification accuracy. Participants were able to earn up to 3000 points and were informed that 1000 points were equivalent to 5€, 2000 points to 10€, and 3000 points to 15€.

Self-Report Task Ratings. During the Effort Valuation Task, participants were probed, via 11-point Likert scales, for cue liking, task difficulty, and subjective experience of fatigue at baseline, as well as two times during each block. Participants were instructed to rate to which degree they liked the 4 reward/effort cues (0= did not like at all, 5= indifferent, 10= liked very much), how tired they felt (0=not tired at all and 10=very tired), and how difficult the High Effort and Low Effort tasks were (0=not difficult at all and 10=very difficult). Ratings for each block were composed of the average of the two block ratings.

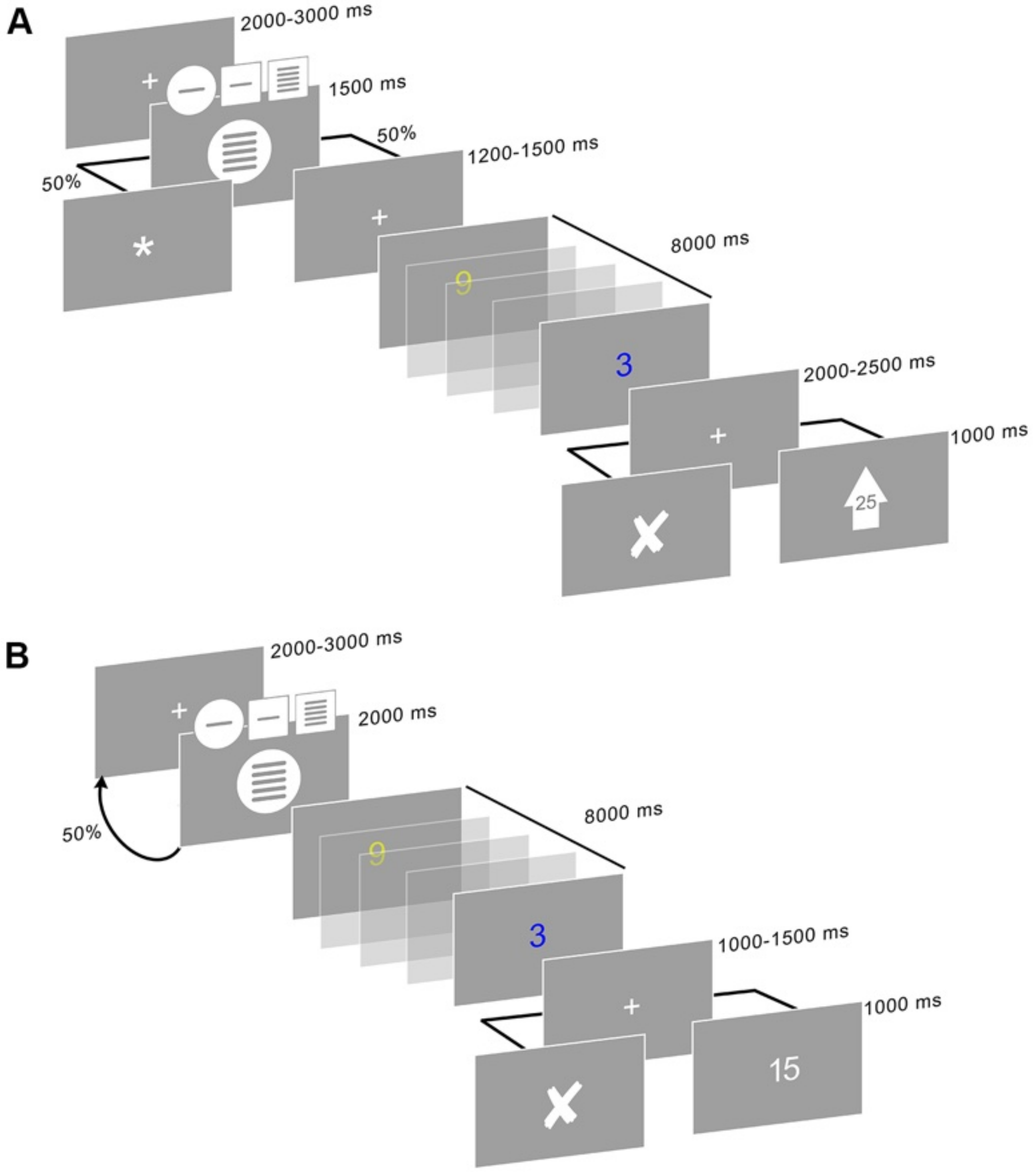


Figure 4.1: A) Schematic of Effort Valuation Task used in Study 1. Note that cues with one line indicate low reward on offer (5 points) while cues with five lines indicate high reward on offer (25 points). **B)** Schematic of the Probabilistic Effort Valuation Task used in Study 2. Note that cues with one line indicate that the trial has high probability of success (less responses are required). Cues with five lines indicate low probability of success (more responses are required).

Training and Calibration. Before beginning the Effort Valuation task, the participants were instructed on the different cue types, trial types, effort task rules, and compensation scheme. Next, participants completed a series of practice trials in blocks for each of the three trial types (e.g. low effort with all blue numbers, low effort with all yellow numbers, and high effort). Participants were told that they needed to correctly complete a minimum of 5 trials before they could move on to the real task. Although effort phases for practice trials were locked to 8 seconds, the cue and feedback presentation were self-paced in order to ensure that subjects understood the meaning of the presented stimuli.

In practice trials, effort tasks were considered unsuccessful if participants a) made more than 2 errors or b) were less than 85% accurate on their decisions in the 8-second window. Data from the practice trials was used to set the initial difficulty of high and low effort tasks. The number of correct decisions for each successful practice trial was stored in an array specific to each of the trial types. The number of correct decisions required to successfully complete a trial ("decision thresholds") for each trial type were then calculated by taking correct number of decisions above the lower 20th percentile. This method effectively fixed success rates of low and hard effort trials to 80%, making it equally probable to obtain reward under both levels of effort demands and minimizing the effect of probability discounting. These arrays were continuously updated during the task so that decision thresholds were recalculated for each trial based on performance on the previous 5 trials of that same trial type. Thus, decision thresholds decreased and increased based on poor or improved performance, respectively, on recent trials. This allowed our task to mitigate the effects of fatigue, which could diminish performance and reduce probability of reward, and learning of the effort task, which would improve performance and thereby increase (differentially) the probability of reward.

End of Session Questionnaire. At the end of the experiment, participants completed a 6-item survey to help us assess their understanding of the paradigm. Specifically, participants had to identify which cue signaled a 5- or 25-point offer and which cue signaled an upcoming high or low effort trial. We also asked participants to rate their perceived accuracy (from 0% to 100%) on the low and high effort tasks, separately.

4.3.1.3 Electroencephalographic activity recording and preprocessing

EEG data was continuously recorded from 33 standard scalp sites (Fp1/2, Fz, F3/4, F7/8, FCz (reference), FC1/2, FC5/6, FT9/10, Cz, C3/4, T7/8, CP1/2, CP5/6, Pz, P3/4, P7/8, O1/2, L/R Mastoids, ground at Fpz electrode) using active electrodes mounted on an ActiCap (Brain Products©). EEG signal was amplified using BrainAmp amplifier, with a continuous sampling at a rate of 250 Hz, with a 0.01 Hz high-pass filter and 50 Hz notch filter. Eye movements were recorded with an electrode at the infraorbital ridge of the right eye. All electrode impedances were kept below 10kΩ.

EEG data were preprocessed and analyzed in MATLAB©using EEGLAB toolbox (Delorme and Makeig, 2004). EEG signals were first re-referenced to the average activity of the two mastoids (L/R). The EEG data were bandpass filtered between 0.01 Hz to 45 Hz. To analyze activity associated with cue and feedback phases, the signals were epoched from -2000 to 2000 ms relative to cue and feedback onset, respectively, with the activity from -200 to 0 ms serving as the baseline. All epoched data were screened manually for artifacts (e.g., spikes, channel-jumps, and non-biological signals). Independent components analysis (ICA) was then applied to the data and components reflecting motion artifacts (i.e. blinks/eye movement) were removed.

Finally, data were visually inspected again and remaining artifacts were removed. Analyses were then conducted on the remaining N=28 subjects (17 female, age: M= 27.89, SD=5.20) with viable EEG data. Due to unequal reward rates in Block 1 (see Behavioral results), analyses were conducted with Block 1 trials removed, resulting in an average of 299.25 trials (SD=10.99) for the cue phase and 117.79 trials (SD=9.45) for the feedback phase.

4.3.2 Study 2

4.3.2.1 Participants

Results from Study 1 suggested that a sample size of N=27 was adequate for detecting medium effect sizes in cue and feedback. However, to ensure that our final sample size was large enough, we recruited 37 healthy adults (20 female, age: M= 24.00, SD=5.77) to participate in Study 2. Two subjects were excluded due to low accuracy (<30%) on the catch identification trials and 3 participants were excluded for excessive motion artifacts, leaving a final sample of N=32.

4.3.2.2 Procedures

The behavioral paradigm and procedures for were similar to Study 1 except for the differences noted below.

Probabilistic Effort Evaluation Task. The paradigm was very similar to the task used in Study 1, but with a few key differences (see Figure 4.1b). First, instead of manipulating reward magnitude, we directly manipulated probability of success. Thus, potential rewards were fixed to 15 points per effort trial, but effort trials either had a high or low probability of success. Probability of success was manipulated by setting the decision threshold higher for low probability trials and lower for high probability trials. Specifically, decision thresholds for High Probability trials were set as in Study 1 (by taking correct number of decisions above the lower 20^{th} percentile from the past 5 trials), while decision thresholds for Low Probability trials were to the number of correct decisions above the 60^{th} percentile. This effectively locked probability to success to above 80% on High Probability trials and below 60% on Low Probability trials.

Second, we simplified the design of the task in the following ways. First, we set the Low Effort task to only one decision type (greater than/less than 5). This was done to simplify instructions and save time on the initial training/calibration. We selected the greater than/less than 5 decision rule because this task was rated as less difficult than the even/odd task, thereby allowing us to maximize the difference between low and high effort demand. Second, since FMT is hypothesized to signal the need to implement control (Cavanagh and Frank, 2014), it is possible that FMT activity in Study 1 was locked to the pre-effort fixation cross instead of the reward/effort cue since the pre-effort fixation was deterministic of future effort. To address this concern, we removed the pre-effort fixation cross from the task in Study 2. Instead, we extended the cue presentation to 2 seconds, which was then directly followed by either the corresponding effort task (work trials) or the next trial (no-work trials). Third, we shortened the pre-feedback ISI to 1000 to 1500 ms (steps of 100ms). All other trial and block structures remained the same as in Study 1. Fourth, we simplified the identification questions by asking participants to identify which cue image (as opposed to the meaning of the cue) was presented in the previous trial.

Self-Report Task Ratings. As in Study 1, participants were probed, via 11-point Likert scales, for cue liking and subjective experience of fatigue at baseline, as well as two times during each block. However, because we expected that probability of success would impact difficulty ratings, we decided to probe participants regarding how much effort was required to complete each task (0=No Effort, 10=Extreme Effort). Further, although participants were explicitly told which cues would signal high vs low probability of success, we also asked participants to rate how likely (0-100%) they were to correctly complete each task. As in Study 1, participants were asked for their ratings after the initial practice phase and twice during each block.

Training and Calibration. In Study 1 we saw that the calibration mechanism took longer than expected in stabilizing probability rates. In order to avoid tossing out the first trials, we extended the practice sessions so that participants had to correctly complete a minimum of at least 15 (as opposed to 5) trials of each effort type. We also interweaved the one-color and two-color tasks (as opposed to practicing in blocks) to better simulate the real task. Initial decision thresholds were based on the last five correct trials.

End of Session Questionnaire. At the end of the experiment, participants completed a 2-item survey to help us assess their understanding of cues and their effort demand contingencies. Specifically, participants had to identify which cue signaled an upcoming high or low effort trial.

4.3.2.3 Electroencephalographic activity recording and preprocessing

EEG data was continuously recorded from 32 standard scalp sites (Fp1/2, Fz (reference), F3/4, F7/8, FC1/2, FC5/6, FT9/10, Cz, C3/4, T7/8, CP1/2, CP5/6, Pz, P3/4, P7/8, O1/2, L/R Mastoids, ground at Fpz) using active electrodes mounted on an ActiCap (Brain Products ©). EEG signal was amplified using BrainAmp amplifier, with a continuous sampling at a rate of 500 Hz, with a 0.01 Hz high-pass filter and 50 Hz notch filter. Eye movements were recorded with an electrode at the infraorbital ridge of the right eye. As in Study 1, all electrode impedances were kept below 10kΩ.

EEG data were preprocessed and analyzed in MATLAB©using EEGLAB toolbox (Delorme and Makeig, 2004). EEG signals were first re-referenced to the average activity of the two mastoids (L/R). The EEG data were bandwith filtered with a bandpass of 0.01 Hz to 45 Hz. To analyze activity associated with cue and feedback phases, the signals were epoched from -2000 to 2000 ms relative to cue and feedback onset, respectively. All epoched data were screened manually for artifacts (e.g., spikes, channel-jumps, and non-biological signals). Independent components analysis (ICA) was then applied to the data and components reflecting motion artifacts (i.e. blinks/eye movement) were removed.

Finally, data were again visually inspected and remaining artifacts were removed. Three subjects were removed for excessive motion artifacts. Analyses were performed on the remaining N=32 subjects (28 female, age: M= 23.93, SD=5.24) with an average of 354.47 trials (SD=33.99) for the cue phase and 130.16 trials (SD=10.37) for the feedback phase.

4.3.3 Data Analysis

4.3.3.1 Event-Related Potentials

EEG data was again low-pass filtered at 20 Hz offline. Components in the cue phase and feedback phase were studied by epoching data time-locked to 200 ms before and 1000 ms after cue and feedback onset, respectively. Time windows and electrode sites for ERP components for each phase were selected by exploring waveforms and topographic maps across all conditions for each study separately. Cue-P3 was defined as the average amplitude from 350 and 500 ms after cue onset for Study 1 and 450 to 550ms after cue onset for Study 2. In Study 1, FB-P3 was defined as the mean activity between 300 and 400 ms following feedback onset, and 350 to 450ms in Study 2.

4.3.3.2 Time Frequency Analysis

Time-frequency analysis was performed per trial in 4 second epochs for cue and feedback phases (2 sec before cue/feedback through 2 sec after). In order to find the induced time-frequency activity, we convoluted single-trial activity using a complex Mortlet wavelet from 1 Hz to 40 Hz using 1Hz steps. We then computed the mean change in power with respect to baseline for each phase, defined as the 400 to 200ms before cue or feedback onset. To compare different conditions, trials associated with a specific Reward/Effort condition were averaged for each participant before performing a grand average. The mean increase/decrease in power for each condition was computed at Fz, Cz and Pz. Based on previous studies implicating theta in both effortful control (Cavanagh and Frank, 2014; Cavanagh and Shackman, 2015), we specifically focused on theta (4-8 Hz) in time windows where the effect of our manipulations appeared maximal (100 to 400 ms after cue and 200 to 550ms after feedback onset for both experiments).

4.3.3.3 Statistical Analysis

Time-frequency analysis was performed per trial in 4 second epochs for cue and feedback phases (2 sec before cue/feedback through 2 sec after). In order to find the induced time-frequency activity, we convoluted single-trial activity using a complex Mortlet wavelet from 1 Hz to 40 Hz using 1Hz steps. We then computed the mean change in power with respect to baseline for each phase, defined as the 400 to 200ms before cue or feedback onset. To compare different conditions, trials associated with a specific Reward/Effort condition were averaged for each participant before performing a grand average. The mean increase/decrease in power for each condition was computed at Fz, Cz and Pz. Based on previous studies implicating theta in both effortful control (Cavanagh and Frank, 2014; Cavanagh and Shackman, 2015), we specifically focused on theta (4-8 Hz) in time windows where the effect of our manipulations appeared maximal (100 to 400 ms after cue and 200 to 550ms after feedback onset for both experiments).

Behavioral Data. The novelty of the Effort Valuation and Probabilistic Effort Valuation tasks were that effort demands were continuously calibrated so that effort could be fully disassociated from reward probability. Thus, it was important for us to confirm that participants had similar success rates between high and low effort trials across the task. Thus, we used linear mixed-effects models (LMM) with Block, Effort, Reward (Study 1)/Probability (Study 2), and their interactions as fixed effects, Subject as a random effect, and trial success as the outcome to test if our calibration mechanism effectively locked success rates throughout the tasks. For our task to be valid, we also needed to confirm that high effort trials were more cognitively demanding than low effort trials. Thus, we used the same fixed and random effects structure to fit two LMMs to the number of decisions made per trial and average speed of decision. Although we expected self-report fatigue to increase with time on task, we designed our calibration mechanism to adjust for declines in reward probability due to fatigue-related diminished performance. Thus, we first fit an LMM with self-report fatigue ratings at the dependent variable, Block as a fixed effect and subject as a random effect to see how fatigue changed throughout the task. We also used another LMM, with fatigue ratings, Block, and their interactions as fixed effects, subject as random effects, to predict block-wise mean trial accuracy.

With respect to self-report ratings, we expected that effort, reward probability, and time on task would affect appetitive responses to the cues (cue-liking) and subjective experience of task difficulty/effort. Again, we used two LMMs, with Block, Effort, Reward (Study 1)/Probability (Study 2), and their interactions as fixed effects and Subject as a random effect, to explore if self-report cue-liking and task difficulty/effort were modulated by our experimental manipulations. In the case of Study 2, we were interested in seeing how our probability manipulation impacted participants' perceived probability of successfully completing a trial. Thus, we first fit an LMM with the same fixed and random effects structure to the self-report probability of success data.

EEG Data. To study the effect of reward magnitude and probability and effort demands on midline ERP amplitudes and theta power, we conducted separate repeated-measures ANOVA with Effort (high and low), Reward Magnitude (high and low; Study 1) or Probability (high and low; Study 2) and Sensor (Fz, Cz, and Pz) as within-participant factors and time-locked ERP components and theta power as dependent measures. The Greenhouse-Geisser correction was applied in cases where the sphericity assumption was violated. Paired sample t-tests with Tukey HSD corrections for multiple comparisons were used to explore significant effects post-hoc. In the case where normality assumptions were violated, Wilcoxon signed rank tests were used.

As discussed below, we detected null effects of Effort, Reward Magnitude, and Reward Probability on cue-related theta power. However, a "non-significant" p-value ($p<.05$) alone does not meaningfully support a null effect (Gelman and Stern, 2012). Bayesian approaches would be better suited to quantify the amount of evidence in favor of the null hypotheses that Effort and Reward Magnitude/Probability do not have effects on theta power at cue. Specifically, we first replicated our original analysis using Bayesian rmANOVA in JASPv0.17.1. In our case, we expected to replicate our original findings such that theta power during the cue phase would be best predicted by a model with only Sensor as a predictor. Bayes Factors (BFs) are computed to compare the probability of an alternative model relative to the probability of the null model. Inclusion Bayes factor ($\mathrm{BF}_{\mathrm{incl}}$), which contrasts the performance of a model with a given predictor against the performance of all models that exclude that predictor, were used to quantify the importance of a given predictor. Finally, we conducted Bayesian paired-sample t-tests to quantify the relative strength of evidence in favor of the simple null hypotheses (H0) that 1) Effort and 2) Reward Magnitude/Probability do not have an effect on theta power at cue. A $\mathrm{BF}_{01}>3$ (or $\mathrm{BF}_{10}<1/3$) is interpreted as moderate evidence in support of the null hypothesis (Wagenmakers et al., 2011).

4.4 Results

4.4.1 Study 1

4.4.1.1 Behavioral and Self-Report Data

The primary aim of our paradigm was to experimentally isolate effort demand from reward probability. Thus, we had to first confirm that the likelihood of successfully completing the task, and therefore obtaining the reward, was equivalent for high and low effort trials throughout the task. LMM revealed significant Reward Magnitude (b=0.19, p<0.001) and Effort and Block interaction (b=-2.05, p=0.008; see Table 4.S1). As can be seen in Figure 4.2a, this interaction effect was driven by differential success rates in high vs low effort trials in Block 1. After exploring cumulative success rates in each subject, we concluded that the calibration mechanism created similar reward rates between high and low effort trials starting in Block 2. Thus, we decided to repeat the analysis excluding trials from Block 1. This LMM yielded non-significant effects of Effort (b= -0.18, p=0.883), Block (b=0.00, p=1.00), and Effort and Block interaction (b= 0.39, p=0.715), suggesting that reward rates were quantitatively similar between high effort (M=78.25%, SD=5.77) and low effort (M=78.44%, SD=5.04) trials. Therefore, trials from the first block were excluded from all remaining EEG analyses (see Study 1 Methods). Further, a significant positive effect of Reward Magnitude was found (b= 0.22, p<0.001), such that participants were overall slightly more accurate on high reward trials (M=80.6%, SD=9.3) than low reward (M=76.1%, SD=9.6) trials. All other Effort, Reward Magnitude, and Block interaction effects were non-significant (all p-values >0.3; see Table 4.S1).

Behavioral indices also indicate that our effort manipulation was effective. For example, if high effort trials were truly more difficult, we would expect that participants would make less judgements in the 8-second time window in high compared to low effort trials. As expected, LMMs revealed that participants were able to make less decisions (b=-2.84, p<0.001), and decide less quickly (b=0.30, p<0.001) in high effort vs low effort trials (see Figure 4.2b and 4.2c; Tables 4.S2 and 4.S3). Furthermore, a significant effect of Block suggests that participants were able to make more decisions (b=0.35, p<0.001) in later blocks. Similarly, reaction times for decisions decreased with more time on task (Block: b=-0.05, p=<0.001), however this drop was more steep for high compared to low effort trials (BlockXEffort: b=-0.03, p=0.015). These data suggest that although probability of success remained relatively fixed in Blocks 2 to 5, participants improved with practice.

In addition to behavioral indices, participants also rated the high effort task as more difficult than the low effort task (b=3.31, p= 0.163). Further, both high and low effort tasks were rated as less difficult as time went on (b=-0.218, p<0.001), presumably due to practice effects (Table 4.S4). Conversely, we were concerned that despite practice-related improvements in the task, participants would perform worse in later trials due to fatigue. The calibration method, however, was designed to mitigate the effect of fatigue on effort performance, so that reward probability would not be dependent on current fatigue state. LMMs revealed that although participants reported increased fatigue with time on task (b=0.73, p<0.001), there was no relationship between fatigue ratings and average block accuracy (b=-0.002, p=0.707; Table 4.S5). Thus, taken together, these findings suggest that our paradigm successfully manipulated effort

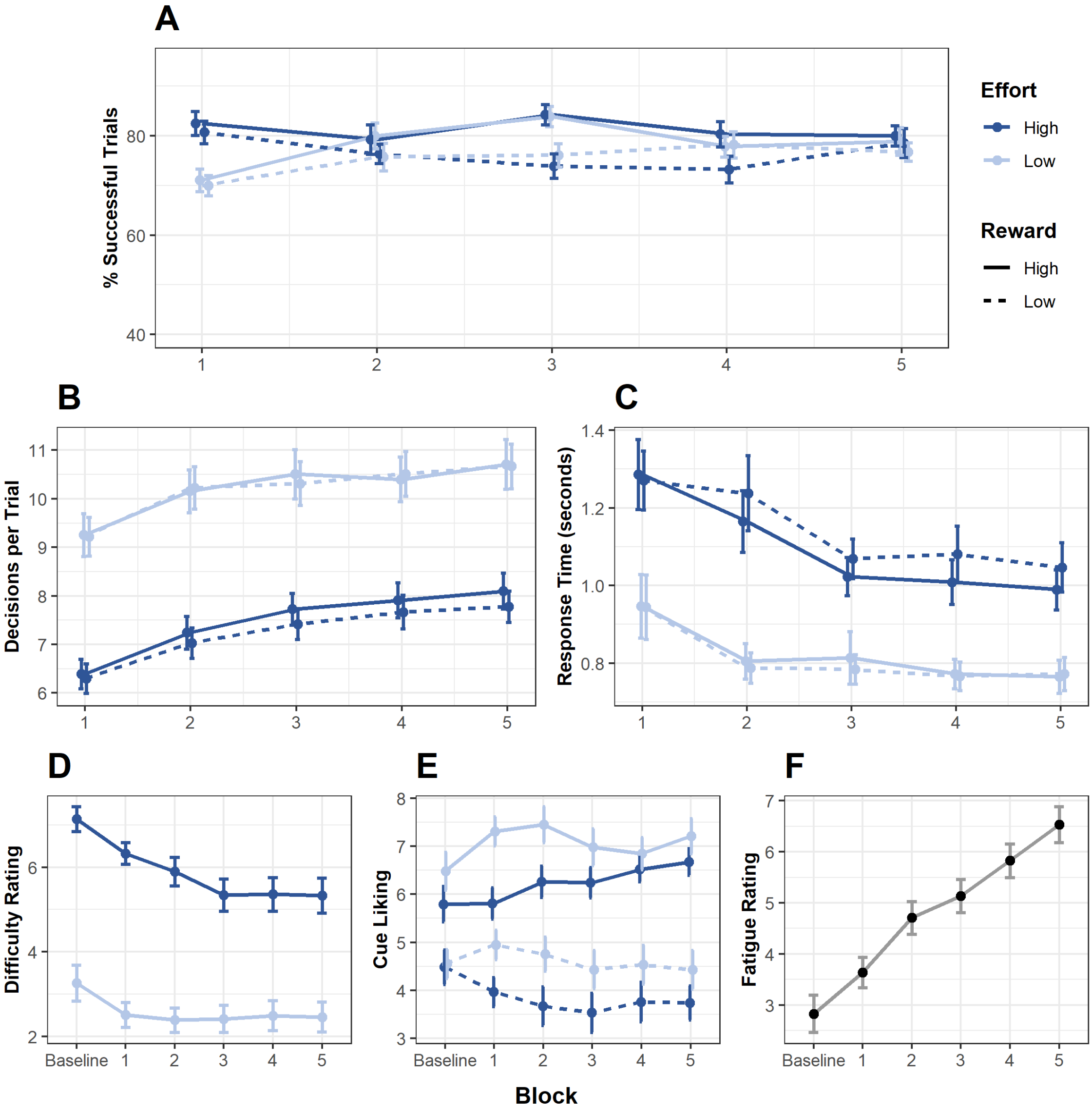


Figure 4.2: Effort Valuation Task adequately manipulates mental effort demands and disassociates it from reward probability. A) Mean percentage of successful trials between high and low effort trials across the task. Success rates for low effort trials are significantly lower in Block 1 than those for high effort trials, but become statistically equivalent in later blocks. **B)** Average number of decisions made in the 8-second time window for high and low effort trials. **C)** Average response time (in seconds) for each decision made in the high vs low effort cue set-switching tasks. **D)** Subjective reports of difficulty for the 2 color (high effort) and 1 color (low effort) task; larger values indicate increased self-report difficulty ratings. Please note that in Study 1, participants were not asked to consider potential reward magnitude when giving difficulty ratings. **E)** Effect of reward and effort on subjective ratings of cue liking; higher values indicate higher appetitive responses to cue. Error bars represent the standard error of the mean. **F)** Self-report ratings of fatigue at each block; larger values indicate increased self-report fatigue ratings.

demand while keeping reward probability constant throughout the task.

As shown in Figure 4.2e, participants also reported liking cues for high reward trials more than low reward trials (b=0.12, p<0.001) and low effort cues significantly more than high effort cues (b=-0.79, p<0.001; Table 4.S1). Moreover, we detected a significant interaction between Reward Magnitude and Block (b=0.01, p=0.003), indicating that high reward cues are liked

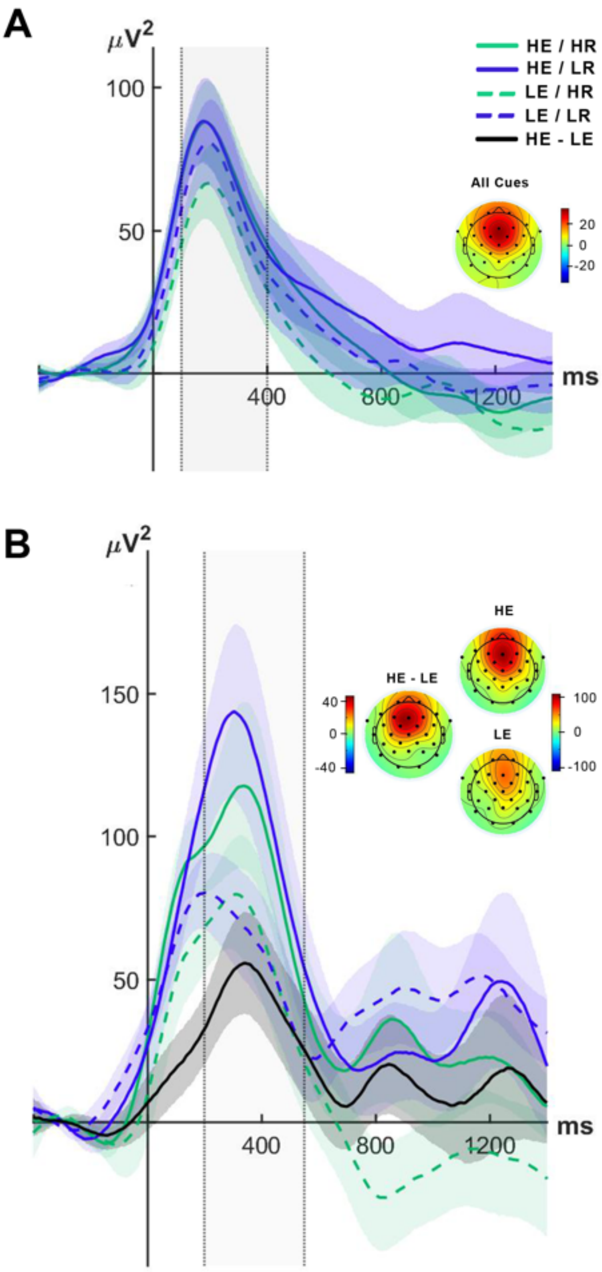


Figure 4.3: FMT during cue evaluation and feedback phases of the Effort Valuation Task. **A)** Time course (in milliseconds) of theta power (μV^2) during cue presentation. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Inset shows the topographic distribution of theta power across all cues 100 to 400ms after cue onset. **B)** Time course (in milliseconds) of theta power (µV2) during correct feedback. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Insets show the topographic distribution of theta power 200 to 300ms after correct feedback onset. **HR**=High Reward, **LR**=Low Reward, **HE**=High Effort, **LE**=Low Effort, **HE-LE**= Difference between High Effort and Low Effort conditions.

more as the task progresses, while liking for low reward cues diminishes with time (see Figure E).

In the end of session questionnaire, 100% of participants correctly identified which cues signaled 5-point, 25-point, low effort, and high effort trials. Overall, participants reported having higher success rates on low (M=75.62%, SD=9.11) compared to high effort trials (M=66.72%, SD=10.46). Wilcoxon signed-rank tests revealed that participants reported being more accurate on low vs high effort trials (Z= -3.13, p= 0.002, r=0.58), despite the fact that real accuracy rates were not different between these conditions.

4.4.1.2 Cue Evaluation Phase

Repeated measures ANOVA revealed a significant effect of sensor at cue (F(1.38, 37.18)=19.82, p<0.001), such that theta was maximal at Fz. However, contrary to our hypothesis, we found no effect of either Reward (F(1, 27)=1.85, p=0.185, η_p^2=0.0) or Effort (F(1, 27)=3.15, p=0.087, η_p^2=0.10) on cue theta (see Figure 4.3a and Table 4.S8). This finding was replicated by model comparison of Bayesian rmANOVAs, which identified that the data was best predicted by a model with Sensor as the sole predictor variable. Averaging across all models there is strong evidence in favor of including Sensor ($\mathrm{BF_{incl}}$=16396.45) and weak evidence of including Effort, Reward Magnitude, and their interactions (all $\mathrm{BF_{incl}}$<0.494; Table 4.S7). Nevertheless, Bayesian pairwise t-tests revealed only anecdotal evidence in favor of a null effect of Effort ($\mathrm{BF_{01}}$= 0.34) and Reward Magnitude ($\mathrm{BF_{01}}$= 2.17). Thus, while FMT was generally present and no effect of Effort or Reward Magnitude were detected, we cannot conclusively deduce that FMT power was not modulated by our task features during the cue evaluation phase.

ERP data, however, suggests that P3 signals reward magnitude of upcoming trial. Specifically, repeated-measures ANOVA detected a significant effect of Reward (F(1, 27)= 43.47, p<0.001, η_p^2=0.62), such that cue-P3 amplitudes were significantly larger for High Reward (M= 4.78, SD=2.34) compared to Low Reward cues (M=3.40, SD=1.87). We also detected significant effects of Sensor (F(1.30, 35.06)= 112.85, p<0.001, η_p^2=0.81), and a significant Reward and Sensor interaction (F(1.32, 35.58)= 18.92, p<0.001, η_p^2=0.41; Table Table 4.S9). As shown in Figure 4.4A, post-hoc pairwise t-tests indicate that cue-P3 amplitudes were significantly larger for High compared to Low Reward cues in parietal and central midline sensors (Cz: t(28)= 5.44, p<0.001, *p-adj.*<0.001; Pz: t(28)=6.36, p<0.001, *p-adj.*<0.001), but that this difference decreased as it approached frontal Fz (t(28)=4.14, p<0.001, *p-adj.*=0.11) Notably, no effect of Effort (F(1,27)=0.24, p=0.63, η_p^2=0.01) or effort-related interactions (EffortXReward: F(1, 27)=0.22, p=0.65, η_p^2=0.01, EffortXSensor: F(1.46, 39.49)=0.12, p=0.82, η_p^2=0.01) were detected, suggesting that expected effort did not enhance cue-related salience.

4.4.1.3 Feedback Phase

In contrast to the cue evaluation phase, both FMT and P3 tracked expended effort at feedback (see Tables 4.S10 and Table 4.S11). Specifically, repeated-measures ANOVA revealed a significant effect of Sensor (F(1.20, 32.35)=9.22, p=0.003, η_p^2=0.26) and an Effort and Sensor interaction (F(1.73, 46.83)=6.18, p=0.006, η_p^2=0.19) on FMT, such that theta power was significantly enhanced for rewards after high compared to low effort at Fz (Z=-2.90, p=0.004, *p-adj.*=0.046, r=0.55), but not Cz (Z=-2.42, p= 0.016, *p-adj.*=0.68, r=0.46) or Pz (Z= -0.91, p=0.362, *p-adj.*=0.99, r=0.17). Figure 4.3b illustrates the effect of effort on theta power at Fz.

Repeated-measures ANOVA also revealed a significant effect of Effort (F(1,27)= 31.95, p<0.001, η_p^2=0.54) and Reward (F(1,27)= 43.94, p<0.001, η_p^2=0.62) on fb-P3. As seen in Figure 4.4B, P3 amplitudes were larger after receiving positive feedback for High (M=13.16, SD=5.13) vs Low Effort (M=10.49, SD=4.00) and for High (M=13.10, SD=4.84) vs Low Reward (M=10.55, SD=4.23). We also detected significant effects of Sensor (F(1.26,33.99)= 35.81, p<0.001, η_p^2=0.57) and a significant Reward and Sensor interaction (F(1.26,34.10)= 9.95, p<0.001, η_p^2=0.27). Post-hoc paired t-tests revealed that although fb-P3 amplitudes were enhanced for high vs low re-

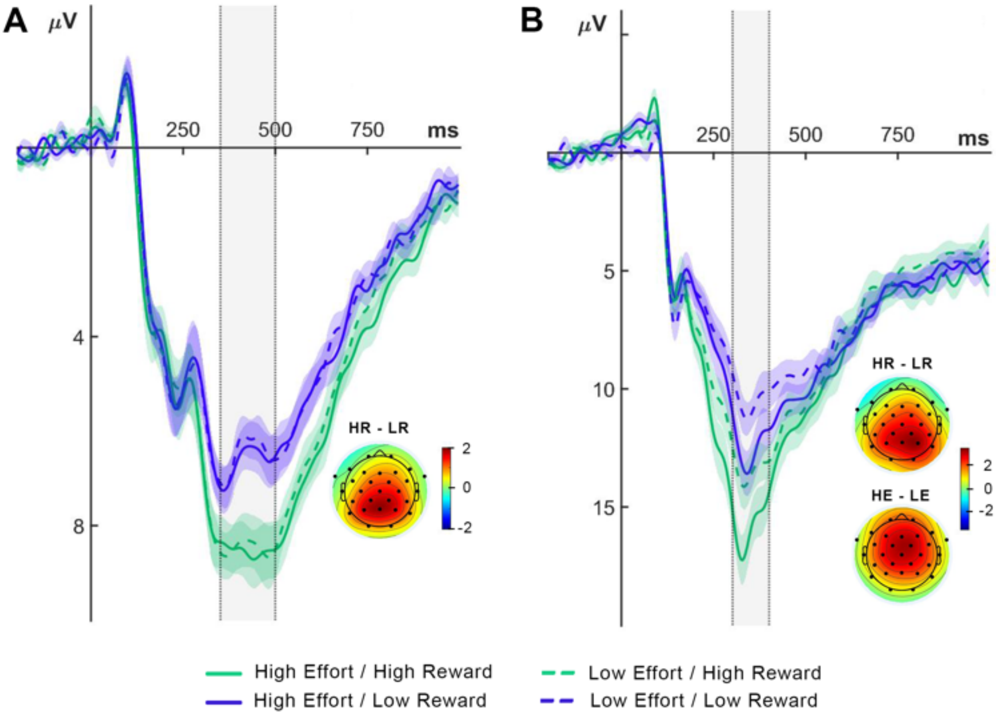


Figure 4.4: P3 during cue evaluation and feedback phases of the Effort Valuation Task. A) Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the cue evaluation phase. **B)** Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the feedback phase. Cue and feedback onset occurred at 0 ms. Shaded regions about the line reflect 95% confidence intervals using between-subjects standard error. Gray shaded regions in the ERP plots indicate the time window used for analysis. Topographic plots reflect the difference in grand averages between conditions in said time regions. HR=High Reward, **LR**=Low Reward, **HE**=High Effort, **LE**=Low Effort, **HR-LR**= Difference between High Reward and Low Reward conditions, **HE-LE**= Difference between High Effort and Low Effort conditions.

wards across all midline sensors, this difference was maximal at Pz (t(27)=8.18, p<0.001, *p-adj.*<0.001). Finally, we also detected a significant effect three-way interaction between Effort, Reward and Sensor (F(1.37, 36.88) = 5.269, p=0.018, η_p^2=0.16), however post-hoc 2x2 repeated measures ANOVAs for each sensor did not yield any significant effect of Effort and Reward (all p-values>0.4), thus we concluded that this interaction was driven by slight differences in the magnitude – but not direction – of reward- and effort-related effects in each sensor.

4.4.2 Study 2

4.4.2.1 Behavioral and Self-Report Data

As in Study 1, we were interested in making sure that success rates were similar between high and low effort trials. In Study 2 however, we also needed to make sure that success rates were significantly higher for high compared to low probability trials. LMM revealed no significant effect of Effort (b=0.16, p=0.869) or Effort and Block interaction (b= -0.30, p=0.658) on success rates (Table 4.S1). As shown in Figure 4.5a, we found a significant positive effect of Probability (b=36.28, p<0.001), such that, on average, participants correctly completed 86.8% (SD=7.2) of high probability trials and 50.5% (SD=11.1) of the low probability trials. Thus, we concluded

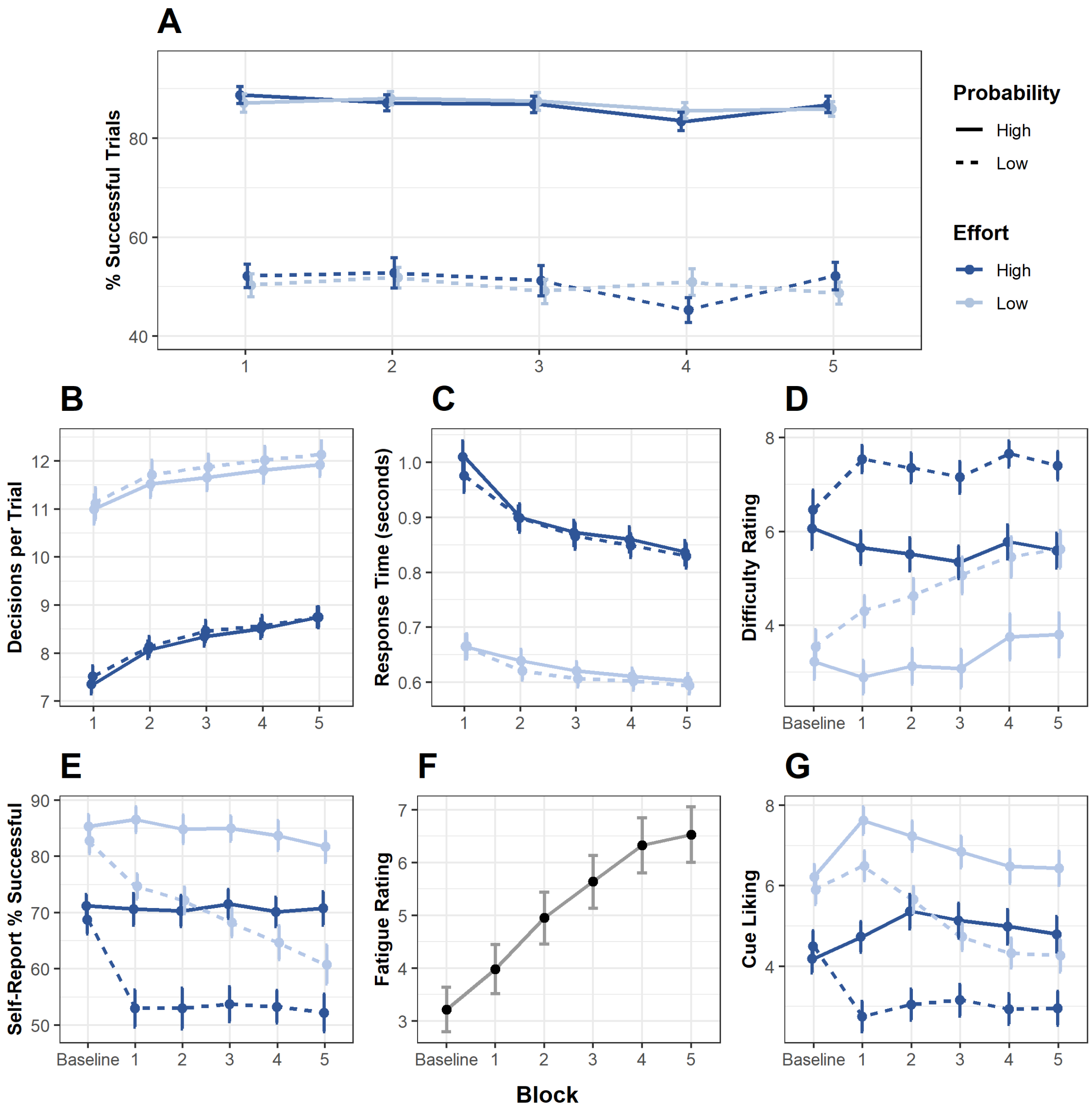


Figure 4.5: Probabilistic Effort Valuation Task adequately manipulates mental effort, but probability of success modulates subjective ratings of difficulty and liking. **A)** Mean percentage of successful trials between high and low probability trials across the task. **B)** Average number of decisions made in the 8-second time window for the different trial types across the task. Participants made more decisions in the high vs low effort trials, and slightly more decisions in low vs high probability trials. **C)** Effect of effort on average response time (in seconds) for each decision made in the different trial types. **D)** Effect of effort and probability of success on subjective reports of task difficulty; larger values indicate increased self-report difficulty. **E)** Effect of effort and probability of success on subjective estimates of the percentage of trials (based on each EffortXProbability condition) that were successfully completed in a given block. **F)** Average self-report ratings of fatigue at each block; larger values indicate increased self-report ratings of fatigue. **G)** Effect of probability and effort on subjective ratings of cue liking; higher values indicate higher appetitive responses to cue. Error bars represent the standard error of the mean.

that 1) the extended practice phase stabilized reward probabilities early in the Probabilistic Effort Valuation Task, thus eliminating the need to exclude trials from the EEG analyses, and 2) that success rates were substantially different between low and high probability trials, regardless of effort type.

We also detected a significant effect of effort type on number of decisions and response time, so that participants in Study 2 made more decisions (b=-3.43, p<0.001) and decided more quickly (b=0.27, p<0.001) in low compared to high effort trials (Figures 5b and c; Tables 4.S2 and Table 4.S3). LMMs also revealed significant Block effects such that participants chose more quickly (b=-0.03, p<0.001) and made more decisions in the 8-second time window (b=0.27, p<0.001) across trial types as the task went on. However, there was a significant effect of Probability (b=-0.13, p=0.04) on number of decisions, such that lower probability of succeeding actually invigorated effortful responding instead of diminishing it.

The high effort task was also rated as more difficult than the low effort task (b=2.42, p<0.001; see Figure 4.5d and Table 4.S4). Probability of success also impacted subjective ratings of difficulty, such that low probability tasks were rated as more difficult than high probability tasks (b=-1.53, p=<0.001). We also detected a significant Probability and Block interaction (b= -0.23, p=0.001), such that high and low probability trials were rated as equally difficult at baseline (before participants experienced the differential success rates), but low probability trials were reported as increasingly effortful throughout the task. We were also interested in knowing if participants were accurately perceiving their probability of success. As expected, participants also reported feeling more likely to succeed in high vs low probability trials (b= 1.45, p<0.001), but only after the baseline period as there were no differences in success probability during the calibration (see Figure 4.5e). Despite having equal success rates across both levels of effort, LMM revealed that participants reported feeling less likely to successfully complete high effort trials than low effort trials (b=-1.43, p<0.001; see Table 4.S7). Subjective ratings of probability of success also significantly decreased with time on task (b=-0.18, p<0.001). This decrease was steeper for low probability (b=0.28, p<0.001) and low effort trials (b=0.12, p=0.011).

As in Study 1, participants reported feeling more fatigued with time on task (b=0.69, p<0.001; see Figure 4.5f and Table 4.S5), but no relationship between fatigue ratings and average block accuracy was detected (b=-0.004, p=0.06). Thus, taken together, these findings suggest that our paradigm successfully manipulated effort demand while keeping reward probability constant throughout the task.

However, unlike Study 1, cue liking ratings in Study 2 generally decreased with time on task (b=-0.16, p=0.001; see Table 4.S6). Probability of successfully completing the task also modulated cue liking, so that high probability cues were generally liked more than low probability cues (b=1.61, p=.137). We also detected a significant Probability and Block interaction (b=0.34, p<0.001). Figure 4.5F illustrates how, despite being explicitly told which cues indicated lower vs higher probabilities of success before baseline measurement, participants initially based cue liking on effort demands alone. With more time on task however, liking for cues indicating lower success ratings began to decline. Finally, 100% of participants correctly identified which cues were associated with high and low effort trials in the end of session questionnaire.

4.4.2.2 Cue Evaluation Phase

ERP and oscillatory patterns in Study 2 are qualitatively similar to those in Study 1. With respect to cue-related theta, repeated measures ANOVA detected a significant effect of sensor at F(1.35, 41.85)=24.85, p<0.001, η_p^2=0.42), but again no effects related to Effort (F(1, 31)= 0.007, p=0.933, η_p^2<0.00), Probability (F(1, 31)=0.68, p=0.417, η_p^2=0.02), or their interactions (Table

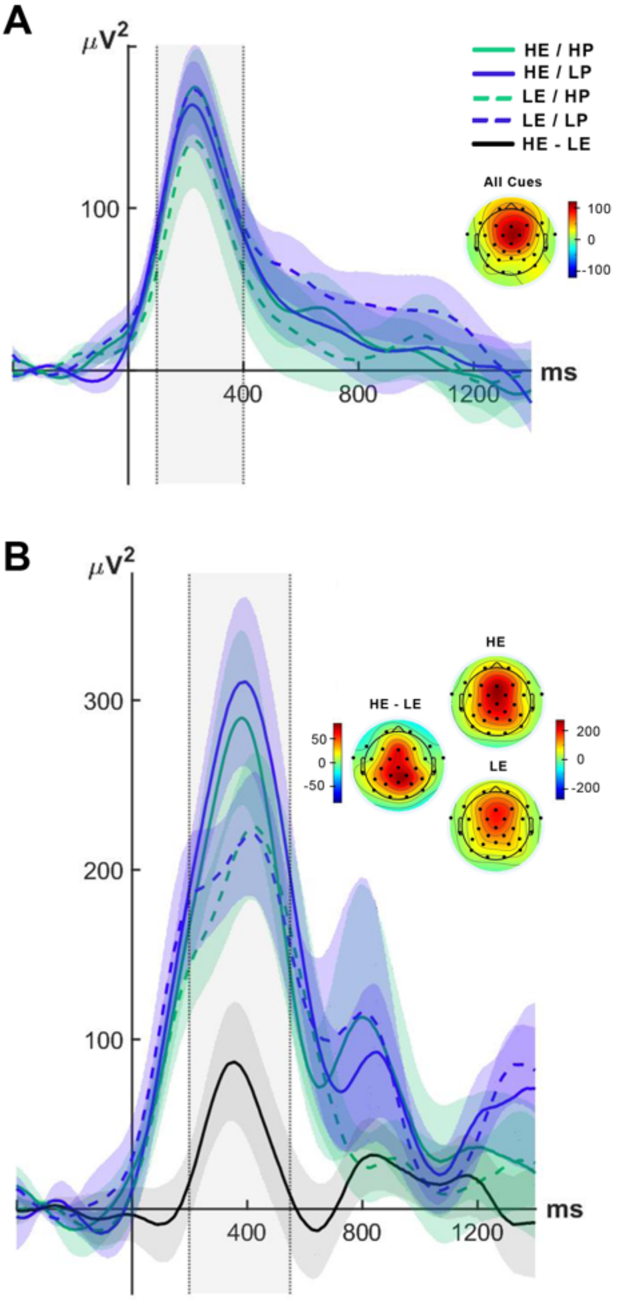


Figure 4.6: FMT during cue evaluation and feedback phases of the Probabilistic Effort Valuation Task. A) Time course (in milliseconds) of theta power (μV^2) during cue presentation. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Inset shows the topographic distribution of theta power across all cues 100 to 400ms after cue onset. **B)** Time course (in milliseconds) of theta power (μV^2) during correct feedback. Shaded regions about the lines represent 95% confidence intervals while the shaded panel represents the time window selected for analysis. Insets show the topographic distribution of theta power 200 to 300ms after correct feedback onset. **HP**=High Probability, **LP**=Low Probability, **HE**=High Effort, **LE**=Low Effort, **HE-LE**= Difference between High Effort and Low Effort conditions.

4.S12). Figure 4.6a shows cue-related theta power activation. Bayesian rmANOVA confirmed that the data best supports a model with only a main effect of Sensor (BF_{10}= 38828.24). Averaging across all models there is strong evidence in favor of including Sensor ($\mathrm{BF}_{\mathrm{incl}}$= 413136.71) and weak evidence of including Effort, Reward Magnitude, and their interactions (all $\mathrm{BF}_{\mathrm{incl}}$<0.169). Bayesian pairwise t-tests revealed strong evidence in favor of a null effect of Effort (BF_{01}= 12.35) and moderate evidence in favor of a null effect of Probability (BF_{01}= 5.13). Thus, we conclude that although FMT was generally present during the cue evaluation phase, it was not modulated by our task manipulations.

Cue-P3 however showed a significant effect of Probability (F(1, 30)= 17.40, p=0.001, η_p^2=0.37), such that cue-P3 amplitudes were significantly greater for Low Probability (M=2.47, SD=2.67) compared to High Probability cues (M=1.82, SD=2.26; see Figure 7a and Table 4.S13). We also detected significant effects of Sensor (F(1.23, 36.78)= 136.51, $p<0.001$, $\eta_p^2=0.82$), and a significant Probability and Sensor interaction (F(1.27, 38.21)= 11.81, $p<0.001$, $\eta_p^2=0.28$). Post-hoc Wilcoxon signed-rank tests and pairwise t-tests indicated that cue-P3 amplitudes were significantly larger for Low compared to High Probability cues in Pz (Pz: Z= -4.31, $p<0.001$, *p-adj.*<0.001, $r=0.76$), but that this difference diminished in more frontal sensors (Fz: t(31)=-2.51, $p=0.017$, *p-adj.*=0.73; Cz: Z= -3.12, $p=0.002$, *p-adj.*=0.053, $r=0.55$). Cue-P3 was not modulated by Effort (F(1,30)=0.44, $p=0.51$, $\eta_p^2=0.01$) or effort-related interactions (EffortXProbability: F(1, 30)=0.02, p=0.90, $\eta_p^2<0.00$, EffortXSensor: F(1.22, 36.63)=0.12, p=0.79, ηp2=0.28), replicating previous results from Study 1.

4.4.2.3 Feedback Phase

In Study 2, repeated measures ANOVA revealed a main effect of Sensor (F(1, 31)=11.59, $p=0.001$, $\eta_p^2=0.27$) and Effort in FMT (F(1, 31)=11.594, $p=0.003$, $\eta_p^2=0.272$), such that FMT was significantly more enhanced across all electrodes for rewards received after exerting High (M=228.03, SD=194.66) compared to Low Effort (M=159.65, SD=156.45). Figure 4.6b displays the effect of effort on FMT power at feedback (see Table 4.S14).

Similarly, repeated-measures ANOVA detected a significant main effect of Effort (F(1, 31)=73.96, $p<0.001$, $\eta_p^2=0.71$), such that fb-P3 amplitudes were significantly greater for rewards after completing High Effort (M=10.89, SD=4.30) compared to a Low Effort trials (M=8.31, SD=4.25; see Figure 4.7b and Table 4.S15). The data also revealed a significant main effect of Probability (F(1, 31)=4.78, $p=0.036$, $\eta_p^2=0.13$) and Sensor (F(1.37, 42.33)=8.95, $p<0.001$, $\eta_p^2=0.22$). Fb-P3 amplitudes were larger when receiving rewards from Low Probability (M=8. 92, SD=4.49) compared to High Probability trials (M=9.59, SD=4.62).

4.5 Discussion

Most goal-directed behavior is mentally costly. Previous studies have implicated the mPFC as a critical structure for tracking both costs and net value representations of effort-based rewards. However, these studies have typically explored the neural correlates of effort-based reward in the context of option comparison (e.g. binary choice paradigms) and without controlling for unequal reward probabilities between effort conditions. The current studies aimed to explore the role of the mPFC in the processing of effort-based reward in the absence of probability discounting. To this end, we used an EEG signal related to cognitive control and reward processing in the mPFC – the FMT – and qualitatively compared this response pattern to an EEG index of incentive salience (P3). Across two studies, we were able to show that our novel paradigm experimentally isolated effort demands from reward probability. EEG data revealed that FMT power was generally enhanced during cue evaluation but did not selectively track upcoming effort demands, reward magnitude or reward probability. At feedback, however, FMT power was sensitive to expended effort, but did not track other reward features. By contrast, during cue presentation, P3 was sensitive to reward magnitude and reward probability, but not effort. At feedback however, P3 amplitudes scaled positively with effort demands, suggesting that expended effort demands increased the salience of reward, but only during the consummatory

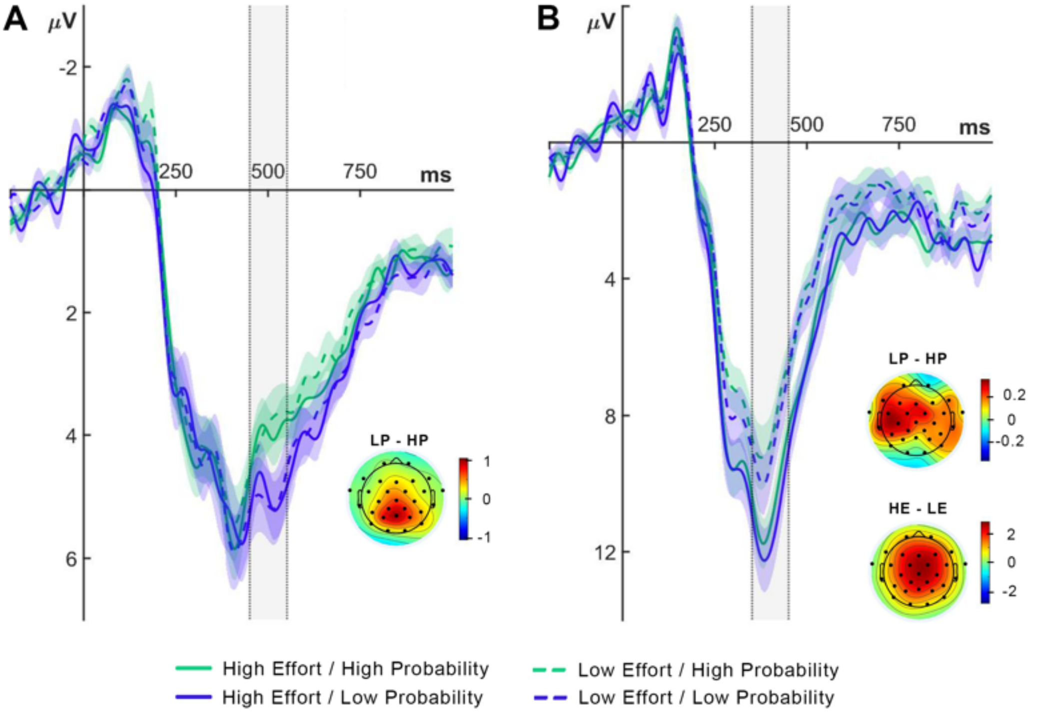


Figure 4.7: P3 during cue evaluation and feedback phases of the Probabilistic Effort Valuation task. **A)** Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the cue evaluation phase. **B)** Time course of grand averages of P3 amplitudes from sensor Fz in each of the four conditions during the feedback phase. Cue and feedback onset occurred at 0 ms. Shaded regions about the line reflect 95% confidence intervals using between-subjects standard error. Gray shaded regions in the ERP plots indicate the time window used for analysis. Topographic plots reflect the difference in grand averages between conditions in said time regions. **HP**=High Probability, **LP**=Low Probability, **HE**=High Effort, **LE**=Low Effort, **LP-HP**= Difference between Low Probability and High Probability conditions, **HE-LE**= Difference between High Effort and Low Effort conditions.

phase. These findings suggest that when reward probabilities are equal between high and low effort conditions, the mPFC does not track net value of prospective effort-based rewards and that expended effort enhances, instead of discounts, the salience of reward at feedback.

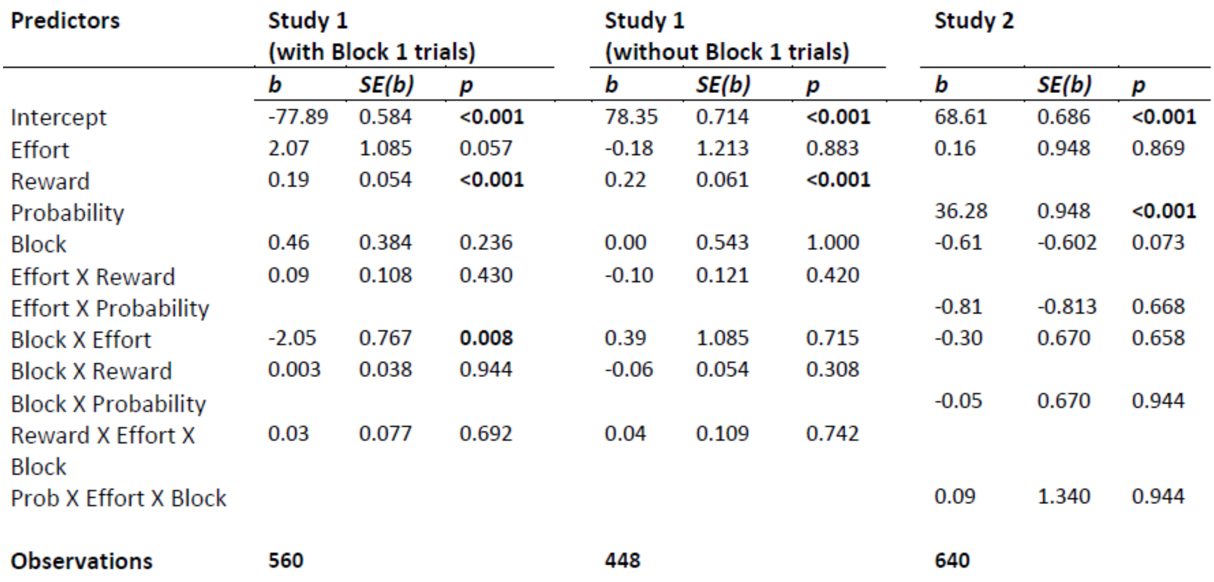
Although the mPFC has been repeatedly implicated in the signaling of effort-based rewards, we did not find any relationship between mPFC function – putatively measured by FMT – and prospective effort demands during the cue evaluation phase. One plausible explanation for this is that the mPFC is only recruited when the environment requires a comparison between more than one option. Previous studies have observed that BOLD in the mPFC/ACC scales positively with effort demands and negatively with the subjective value of effort-based rewards (Chong et al., 2017; Klein-Flugge et al., 2016; Massar et al., 2015; Prévost et al., 2010; Skvortsova et al., 2014). However, these studies used paradigms that required participants to decide between two effort-based rewards, making it difficult to disentangle whether the ACC was signaling net value or exerting cognitive control to facilitate decision-making and action selection. Notably, studies that have experimentally isolated decision difficulty have shown that mPFC/ACC activity scales positively with decision difficulty and single offer net value (Westbrook et al., 2019), but not effort demand (Hogan et al., 2019) or foraging value (Shenhav et al., 2014). Similarly, increased phasic FMT was associated with greater probability of selecting the high-effort choice in physical effort-based reward task, but only in difficult decision trials (Umemoto et al., 2022). The two studies that used paradigms without choice reported mixed results: only one reported that ACC activity scaled with net value (Croxson et al., 2009) and neither detected a relationship between ACC BOLD and prospective effort (Croxson et al., 2009; Stoppel et al., 2011). In our studies, FMT was enhanced during cue evaluation, but was not sensitive to net value or any of the features of prospective effortful reward. The absence of a net value signal in cue-FMT, however, cannot be attributed to a lack of saliency in our effort or reward manipulations. In fact, across both of our studies, increased effort demands attenuated self-report cue liking, suggesting that prospective effort was indeed integrated into estimates of subjective value. Nevertheless, in the absence of alternative options and the need for action selection, FMT did not signal subjective value. Thus, our findings indirectly lend support to a growing body of evidence that suggests that the mPFC/ACC tracks cognitive control requirements of weighing options (Kolling et al., 2016) or guiding action selection (Holroyd and McClure, 2015) rather than net value per se.

At feedback, however, FMT selectively tracked expended effort, but not reward magnitude or probability. This finding is consistent with a previous findings that BOLD activity in the ACC is augmented for increased attentional and cognitive effort demands, but not integrated net value, at reward feedback (Hernandez Lallement et al., 2014; Stoppel et al., 2011). Our findings are also in line with proposals that the mPFC/dACC responds selectively to the value of events that are specifically relevant to the allocation of control (Shenhav et al., 2013). In our paradigm, the difficulty of the effort demands was continuously calibrated through the task. Because reward magnitude and probability of successful outcome were fixed, feedback was only informative about the degree to which previously expended effortful control adequately met the effort demand for that specific trial. Thus, FMT power in positive feedback could feasibly reflect performance monitoring or action value updating, both functions that have been previously attributed to theta band oscillations generated in the ACC (Luft, 2014; Ullsperger et al., 2014). Alternatively, self-report ratings in Study 2 suggest that despite equal reward probabilities across effort conditions, participants generally perceived having a higher probability of success on low compared to high effort trials. Since FMT has been shown to index unsigned prediction errors (Cavanagh et al., 2012; Mas-Herrero and Marco-Pallarés, 2014; Rawls et al., 2020), one possible explanation for enhanced FMT at high effort feedback could be that rewards obtained through more effort are perceived as less likely and therefore unexpected. However, if this were the case, we would expect theta power to have been potentiated for reward feedback in low probability trials as well. To conclusively test the role of theta in effort-based prediction error and performance monitoring, future experiments should use paradigms that directly manipulate reward likelihood as a function of effort demand.

Our findings also show that FMT signals are distinct and separable from signals of incentive salience (cue-P3). Unlike FMT, cue-P3 amplitudes were sensitive to prospective reward magnitude and probability. This is consistent with previous studies that show that cue-P3 amplitudes are modulated not only by reward magnitude, but also reward probability (Schutte et al., 2019), and task efficacy (Frömer et al., 2021), which were controlled in our paradigm. At feedback, however, increased effort demand enhanced P3 responses for positive outcomes, suggesting that expended effort increased the incentive salience of received rewards. These findings are in line with previous findings that suggest that exerted effort amplifies reward saliency signals in human (Ma et al., 2014; Schevernels et al., 2016; Schevernels et al., 2014; Wang et al., 2017) and non-human primates (S. Tanaka et al., 2019). Furthermore, unlike previous studies, the tasks used in the current experiments equalized performance outcomes and reward likelihood between effort conditions. Therefore, we can conclude that effort-related differences in fb-P3 were driven primarily by expended effort and not by other factors, such as reward expectancy or likelihood, which modulate P3 amplitudes (Hajcak et al., 2005; Hajcak et al., 2007; Wu and Zhou, 2009).

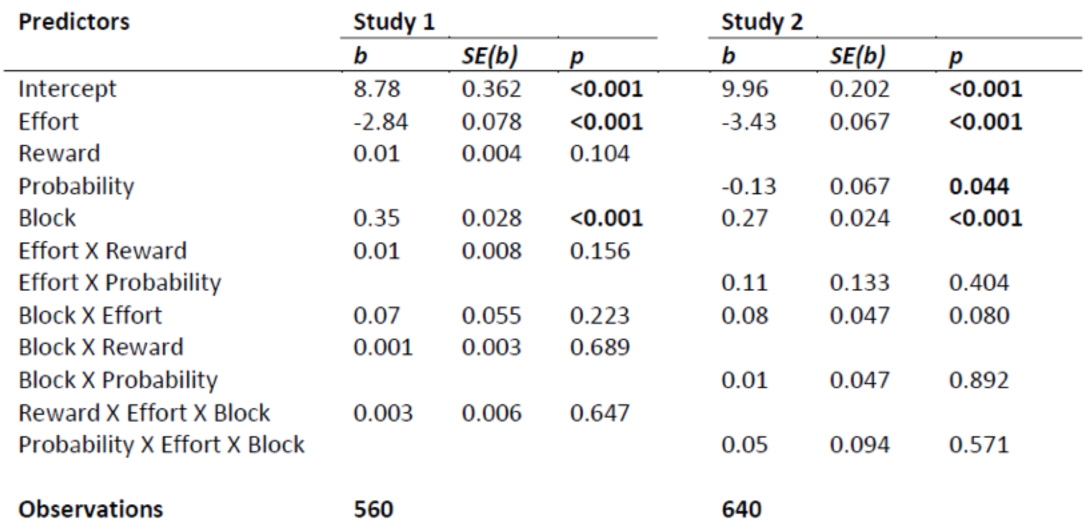
Despite the strengths of our paradigm, there were some limitations to the design. As stated earlier, analyses were limited to successful trials due to the relatively high success rate (achieved via the calibration), thus we could not explore the role of FMT in tracking performance in the context of failure or non-reward. Second, the mPFC is a highly heterogenous region that has been linked to a variety of cognitive control and outcome-processing functions (Clithero and Rangel, 2014; Domenech and Koechlin, 2015; Vassena, Holroyd, et al., 2017). Although the high temporal resolution of EEG was useful for the purposes of our study, combined fMRI-EEG or magnetoencephalography would be well-suited for exploring how the specific subregions of the mPFC contribute to effort-based reward processing. In summary, in two studies we showed that in the absence of alternative options/choice and different reward probability rates, the FMT did not track features of prospective effort-based reward. Instead, FMT power was only enhanced for successful high effort outcomes, which suggests that the mPFC plays a more general performance-monitoring role as opposed to tracking pure cognitive control demands or integrated net value representations. Further, we showed that P3 amplitudes were sensitive to reward magnitude and probability, but not effort, during cue evaluation and that effort enhanced P3 amplitudes to reward at feedback, again suggesting that effort increased the incentive salience of a reward. Understanding how effort-based reward is processed is crucial for understanding psychopathological conditions marked by altered reward motivation, such as Parkinson's disease (Chong et al., 2015; McGuigan et al., 2019), depression (Hammar et al., 2011; M. T. Treadway, Bossaller, et al., 2012; M. T. Treadway et al., 2015), schizophrenia (Barch et al., 2014; Cooper et al., 2019), substance use disorders (Leventhal et al., 2008), and attention-deficit/hyperactivity disorder (Egeland et al., 2010). However, these states of amotivation can be caused by deficits in one or several components of effort-based reward processing, such as reduced salience of prospective and obtained rewards, dysfunctional weighing of prospective cognitive control demands, misallocation of control, and/or deficits in performance monitoring. Thus, novel paradigms are needed to reduce the influence of confounds when investigating the key processing stages effort-based reward. This study paves the way towards that goal.

4.6 Supplementary Tables



Predictors	Study 1 (with Block 1 trials)			Study 1 (without Block 1 trials)			Study 2		
	b	*SE(b)*	*p*	*b*	*SE(b)*	*p*	*b*	*SE(b)*	*p*
Intercept	-77.89	0.584	**<0.001**	78.35	0.714	**<0.001**	68.61	0.686	**<0.001**
Effort	2.07	1.085	0.057	-0.18	1.213	0.883	0.16	0.948	0.869
Reward	0.19	0.054	**<0.001**	0.22	0.061	**<0.001**			
Probability							36.28	0.948	**<0.001**
Block	0.46	0.384	0.236	0.00	0.543	1.000	-0.61	-0.602	0.073
Effort X Reward	0.09	0.108	0.430	-0.10	0.121	0.420			
Effort X Probability							-0.81	-0.813	0.668
Block X Effort	-2.05	0.767	**0.008**	0.39	1.085	0.715	-0.30	0.670	0.658
Block X Reward	0.003	0.038	0.944	-0.06	0.054	0.308			
Block X Probability							-0.05	0.670	0.944
Reward X Effort X Block	0.03	0.077	0.692	0.04	0.109	0.742			
Prob X Effort X Block							0.09	1.340	0.944
Observations	**560**			**448**			**640**		

Table 4.S1: Effects of reward/probability, effort, and block on average success rate (%).



Predictors	Study 1			Study 2		
	b	*SE(b)*	*p*	*b*	*SE(b)*	*p*
Intercept	8.78	0.362	**<0.001**	9.96	0.202	**<0.001**
Effort	-2.84	0.078	**<0.001**	-3.43	0.067	**<0.001**
Reward	0.01	0.004	0.104			
Probability				-0.13	0.067	**0.044**
Block	0.35	0.028	**<0.001**	0.27	0.024	**<0.001**
Effort X Reward	0.01	0.008	0.156			
Effort X Probability				0.11	0.133	0.404
Block X Effort	0.07	0.055	0.223	0.08	0.047	0.080
Block X Reward	0.001	0.003	0.689			
Block X Probability				0.01	0.047	0.892
Reward X Effort X Block	0.003	0.006	0.647			
Probability X Effort X Block				0.05	0.094	0.571
Observations	**560**			**640**		

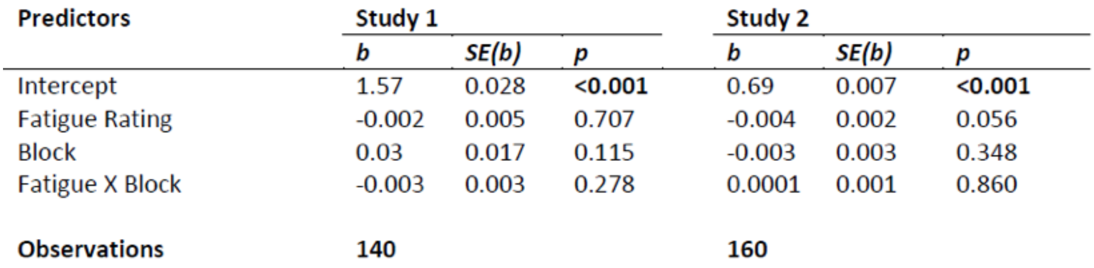
Table 4.S2: Effects of reward/probability, effort, and block on number of choices per trial.

Predictors	**Study 1**			**Study 2**		
	b	***SE(b)***	***p***	***b***	***SE(b)***	***p***
Intercept	0.97	-0.051	**<0.001**	0.76	0.017	**<0.001**
Effort	0.30	-0.017	**<0.001**	0.27	0.006	**<0.001**
Reward	-9.31	0.001	0.279			
Probability				0.01	0.006	0.086
Block	-0.05	0.006	**<0.001**	-0.03	0.002	**<0.001**
Effort X Reward	-0.003	0.002	0.101			
Effort X Probability				0.002	0.012	0.866
Block X Effort	-0.03	0.012	**0.015**	-0.02	0.004	**<0.001**
Block X Reward	<0.00	0.001	0.479			
Block X Probability				-0.002	0.004	0.670
Reward X Effort X Block	<0.00	0.001	0.641			
Probability X Effort X Block				-0.006	0.009	0.511
Observations	**560**			**640**		

Table 4.S3: Effects of reward/probability, effort, and block on average choice speed.

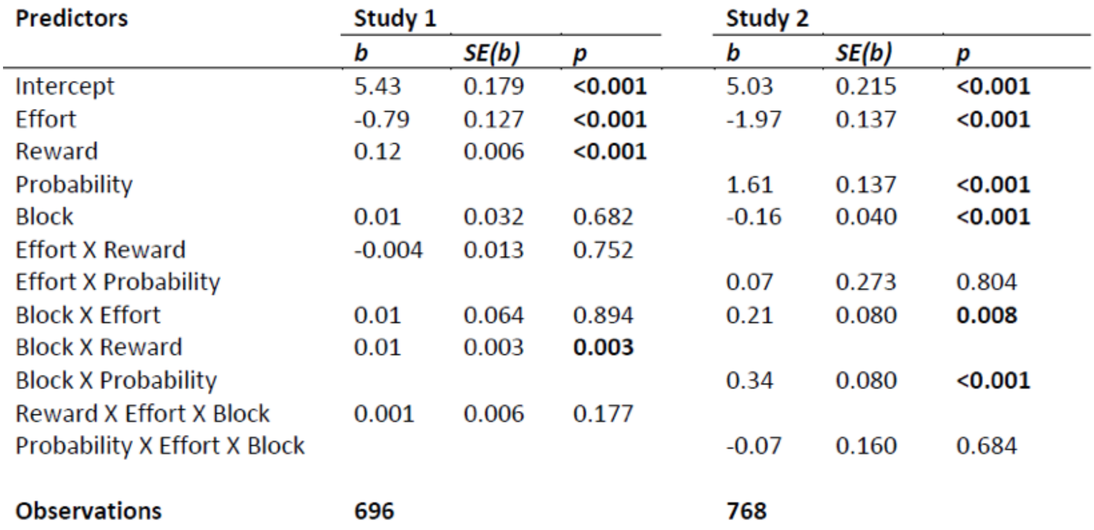
Predictors	**Study 1**			**Study 2**		
	b	***SE(b)***	***p***	***b***	***SE(b)***	***p***
Intercept	4.24	0.217	**<0.001**	5.25	0.242	**<0.001**
Effort	3.31	0.163	**<0.001**	2.42	0.120	**<0.001**
Probability				-1.53	0.120	**<0.001**
Block	-0.22	0.041	**<0.001**	0.16	0.035	**<0.001**
Effort X Block	-0.21	0.082	**0.013**	-0.24	0.070	0.529
Effort X Probability				-0.15	0.240	**0.001**
Probability X Block				-0.23	0.070	**0.001**
Effort X Probability X Block				0.06	0.141	0.684
Observations	**348**			**768**		

Table 4.S4: Effects of effort (and probability) on self-report ratings of difficulty.



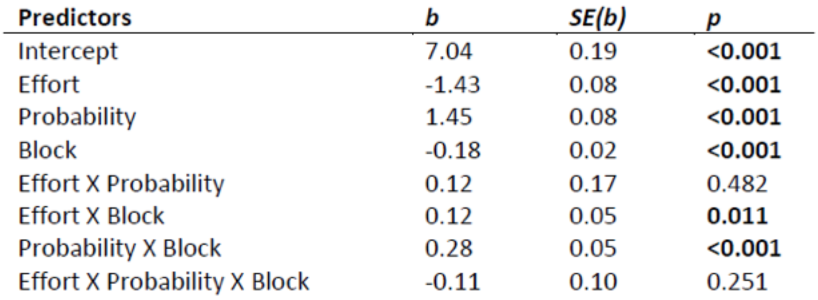
Predictors	**Study 1**			**Study 2**		
	b	***SE(b)***	***p***	***b***	***SE(b)***	***p***
Intercept	1.57	0.028	**<0.001**	0.69	0.007	**<0.001**
Fatigue Rating	-0.002	0.005	0.707	-0.004	0.002	0.056
Block	0.03	0.017	0.115	-0.003	0.003	0.348
Fatigue X Block	-0.003	0.003	0.278	0.0001	0.001	0.860
Observations	**140**			**160**		

Table 4.S5: Effects of self-report fatigue on accuracy



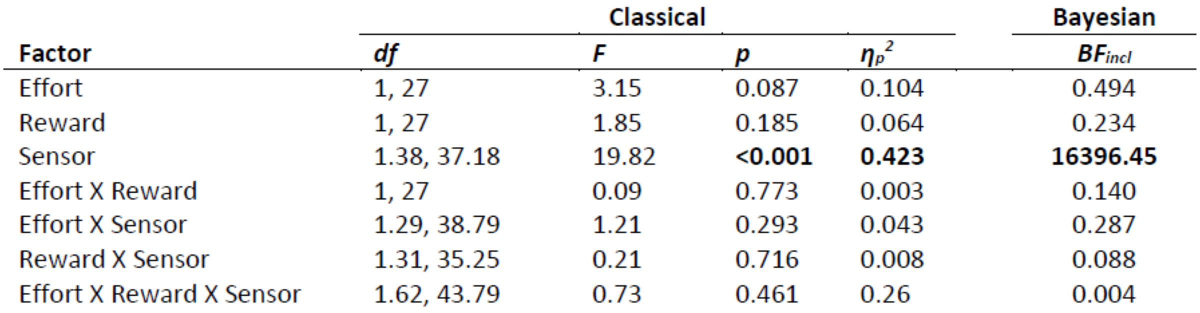
Predictors	**Study 1**			**Study 2**		
	b	***SE(b)***	***p***	***b***	***SE(b)***	***p***
Intercept	5.43	0.179	**<0.001**	5.03	0.215	**<0.001**
Effort	-0.79	0.127	**<0.001**	-1.97	0.137	**<0.001**
Reward	0.12	0.006	**<0.001**			
Probability				1.61	0.137	**<0.001**
Block	0.01	0.032	0.682	-0.16	0.040	**<0.001**
Effort X Reward	-0.004	0.013	0.752			
Effort X Probability				0.07	0.273	0.804
Block X Effort	0.01	0.064	0.894	0.21	0.080	**0.008**
Block X Reward	0.01	0.003	**0.003**			
Block X Probability				0.34	0.080	**<0.001**
Reward X Effort X Block	0.001	0.006	0.177			
Probability X Effort X Block				-0.07	0.160	0.684
Observations	**696**			**768**		

Table 4.S6: Effects of reward/probability, effort, and block on self-report cue liking.



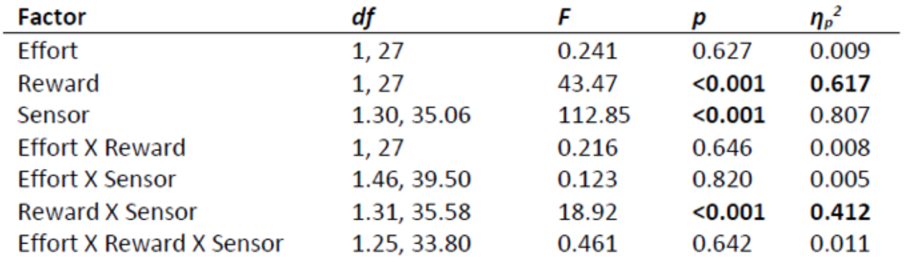
Predictors	***b***	***SE(b)***	***p***
Intercept	7.04	0.19	**<0.001**
Effort	-1.43	0.08	**<0.001**
Probability	1.45	0.08	**<0.001**
Block	-0.18	0.02	**<0.001**
Effort X Probability	0.12	0.17	0.482
Effort X Block	0.12	0.05	**0.011**
Probability X Block	0.28	0.05	**<0.001**
Effort X Probability X Block	-0.11	0.10	0.251

Table 4.S7: Effects of probability, effort, and block on self-report probability of success.



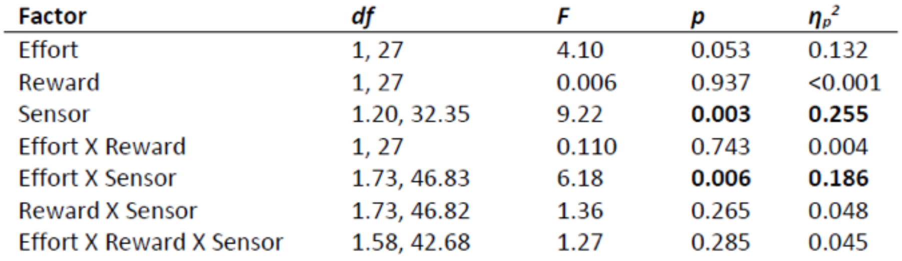
	Classical				**Bayesian**
Factor	***df***	***F***	***p***	η_p^2	BF_{incl}
Effort	1, 27	3.15	0.087	0.104	0.494
Reward	1, 27	1.85	0.185	0.064	0.234
Sensor	1.38, 37.18	19.82	**<0.001**	**0.423**	**16396.45**
Effort X Reward	1, 27	0.09	0.773	0.003	0.140
Effort X Sensor	1.29, 38.79	1.21	0.293	0.043	0.287
Reward X Sensor	1.31, 35.25	0.21	0.716	0.008	0.088
Effort X Reward X Sensor	1.62, 43.79	0.73	0.461	0.26	0.004

Table 4.S8: Results of rmANOVAs for cue theta power (Study 1).



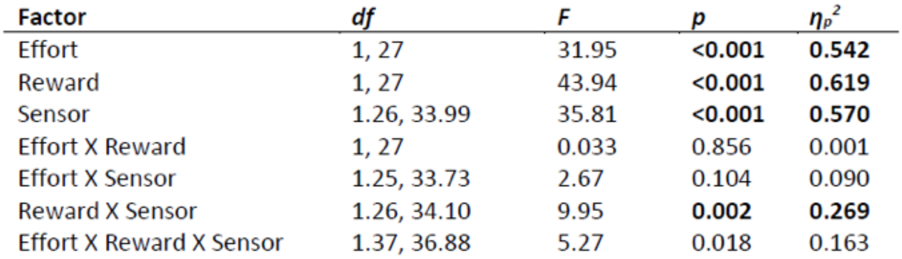
Factor	***df***	***F***	***p***	***η_p^2***
Effort	1, 27	0.241	0.627	0.009
Reward	1, 27	43.47	**<0.001**	**0.617**
Sensor	1.30, 35.06	112.85	**<0.001**	0.807
Effort X Reward	1, 27	0.216	0.646	0.008
Effort X Sensor	1.46, 39.50	0.123	0.820	0.005
Reward X Sensor	1.31, 35.58	18.92	**<0.001**	**0.412**
Effort X Reward X Sensor	1.25, 33.80	0.461	0.642	0.011

Table 4.S9: Results of rmANOVA for cue-P3 amplitudes (Study 1).



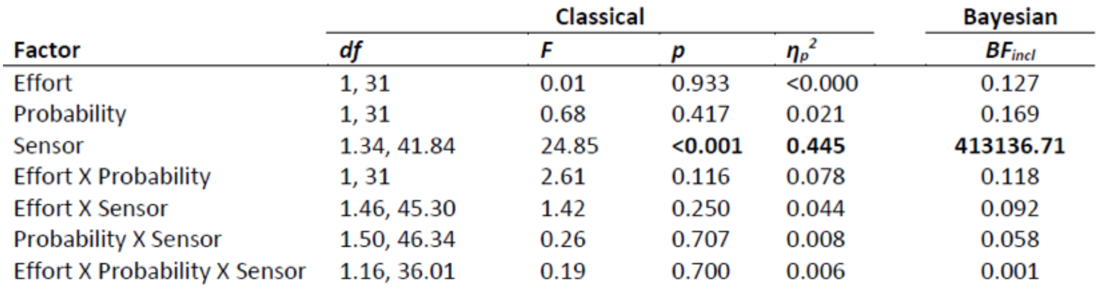
Factor	***df***	***F***	***p***	***η_p^2***
Effort	1, 27	4.10	0.053	0.132
Reward	1, 27	0.006	0.937	<0.001
Sensor	1.20, 32.35	9.22	**0.003**	**0.255**
Effort X Reward	1, 27	0.110	0.743	0.004
Effort X Sensor	1.73, 46.83	6.18	**0.006**	**0.186**
Reward X Sensor	1.73, 46.82	1.36	0.265	0.048
Effort X Reward X Sensor	1.58, 42.68	1.27	0.285	0.045

Table 4.S10: Results of rmANOVAs for FB theta power (Study 1).



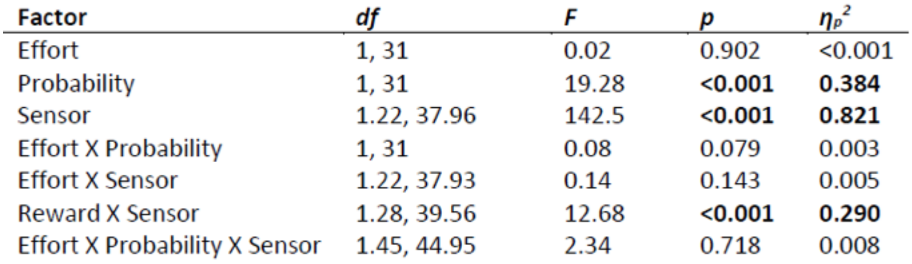
Factor	***df***	***F***	***p***	η_p^2
Effort	1, 27	31.95	**<0.001**	**0.542**
Reward	1, 27	43.94	**<0.001**	**0.619**
Sensor	1.26, 33.99	35.81	**<0.001**	**0.570**
Effort X Reward	1, 27	0.033	0.856	0.001
Effort X Sensor	1.25, 33.73	2.67	0.104	0.090
Reward X Sensor	1.26, 34.10	9.95	**0.002**	**0.269**
Effort X Reward X Sensor	1.37, 36.88	5.27	0.018	0.163

Table 4.S11: Results of rmANOVA for FB-P3 amplitudes (Study 1).



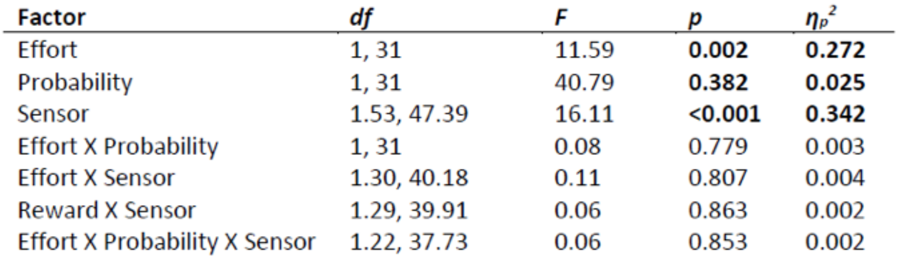
	Classical				**Bayesian**
Factor	***df***	***F***	***p***	η_p^2	BF_{incl}
Effort	1, 31	0.01	0.933	<0.000	0.127
Probability	1, 31	0.68	0.417	0.021	0.169
Sensor	1.34, 41.84	24.85	**<0.001**	**0.445**	**413136.71**
Effort X Probability	1, 31	2.61	0.116	0.078	0.118
Effort X Sensor	1.46, 45.30	1.42	0.250	0.044	0.092
Probability X Sensor	1.50, 46.34	0.26	0.707	0.008	0.058
Effort X Probability X Sensor	1.16, 36.01	0.19	0.700	0.006	0.001

Table 4.S12: Results of rmANOVAs for cue theta power (Study 2).



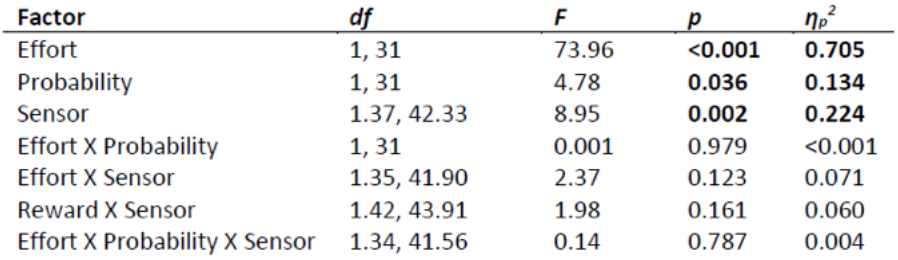
Factor	***df***	***F***	***p***	η_p^2
Effort	1, 31	0.02	0.902	<0.001
Probability	1, 31	19.28	**<0.001**	**0.384**
Sensor	1.22, 37.96	142.5	**<0.001**	**0.821**
Effort X Probability	1, 31	0.08	0.079	0.003
Effort X Sensor	1.22, 37.93	0.14	0.143	0.005
Reward X Sensor	1.28, 39.56	12.68	**<0.001**	**0.290**
Effort X Probability X Sensor	1.45, 44.95	2.34	0.718	0.008

Table 4.S13: Results of rmANOVA for cue-P3 amplitudes (Study 2).



Factor	***df***	***F***	***p***	η_p^2
Effort	1, 31	11.59	**0.002**	**0.272**
Probability	1, 31	40.79	**0.382**	**0.025**
Sensor	1.53, 47.39	16.11	**<0.001**	**0.342**
Effort X Probability	1, 31	0.08	0.779	0.003
Effort X Sensor	1.30, 40.18	0.11	0.807	0.004
Reward X Sensor	1.29, 39.91	0.06	0.863	0.002
Effort X Probability X Sensor	1.22, 37.73	0.06	0.853	0.002

Table 4.S14: Results of rmANOVA for FB theta amplitudes (Study 2).



Factor	***df***	***F***	***p***	**η_p^2**
Effort	1, 31	73.96	**<0.001**	**0.705**
Probability	1, 31	4.78	**0.036**	**0.134**
Sensor	1.37, 42.33	8.95	**0.002**	**0.224**
Effort X Probability	1, 31	0.001	0.979	<0.001
Effort X Sensor	1.35, 41.90	2.37	0.123	0.071
Reward X Sensor	1.42, 43.91	1.98	0.161	0.060
Effort X Probability X Sensor	1.34, 41.56	0.14	0.787	0.004

Table 4.S15: Results of rmANOVA for FB-P3 amplitudes (Study 2).

Chapter 5

Performance Feedback, but Not Cognitive Effort, Modulates Reward Learning

5.1 Abstract

The tracking of reward prediction and learned reward values recruits the same neural circuitry as the processing of effort-based rewards. Effort demands have been shown to positively shift reward prediction errors and potentiate the learning of stimulus-reward associations (Jarvis et al., 2022; S. Tanaka et al., 2019). These findings contradict accounts that rewards that are more costly are less subjectively valuable, and therefore less reinforcing than rewards that require less effort to obtain. Furthermore, these studies were either used non-human primates or physical effort costs, and did not account for the role of performance feedback in learning. To address this gap, participants (N=28) completed a behavioral paradigm in which they learned stimulus-reward contingencies through experience and received rewards only after successfully completing a cognitively effortful task. Behavioral performance and self-report measures suggest that our task effectively manipulated cognitive effort demands and that participants were able to adapt their choice preferences based on shifting values of reward-predicting cues. However, the study found no evidence that learning rates were modulated by paid effort costs. Instead, learning rates were influenced by performance feedback, such that reward values were updated more efficiently based on successful task execution and actual reward attainment, rather than unsuccessful task execution. These findings suggest that positive performance outcomes, rather than effort costs, may potentiate reward value and that this in turn guides action-outcome learning.

5.2 Introduction

Prominent models of cognitive neuroscience posit that effort is costly and that humans and animals prefer pursuing rewards that require less effort to obtain (Salamone et al., 2018; Zald and Treadway, 2017). In contrast, several studies have shown that more value is allocated to rewards earned from exerting more effort (Alessandri et al., 2008; Clement et al., 2000; Hernandez Lallement et al., 2014; Ma et al., 2014). This “effort paradox” (Inzlicht et al., 2018) highlights the dissociation between how rewards are valued and represented at the time of prediction and choice versus how they are valued upon delivery. While significant advances have been made in elucidating the neural substrates implicated in the processing of effort-based rewards, it remains unclear how effort modulates the learned value of rewards.

The mesocorticolimbic circuit has been consistently implicated in reward learning (RL) and prediction. Dopaminergic midbrain neurons encode reward prediction errors (RPE), or the difference between expected and actual rewards, which serve as a teaching signal in the learning of reward-outcome contingencies (Bayer and Glimcher, 2005; Schultz et al., 2015; Tobler et al., 2005). In rodents, midbrain projections to the striatum have been shown to be important for generating both stimulus–outcome and stimulus–response associations (Balleine et al., 2007; Cox and Witten, 2019; Saunders et al., 2018).These results have been mirrored in humans, with several studies showing that dopamine-dependent mechanisms enhance reinforcement learning signals in the striatum (Cox and Witten, 2019; Diederen et al., 2017; Jocham et al., 2011). Striatal projections to prefrontal areas, particularly the medial prefrontal cortex (mPFC) and anterior cingulate cortex (ACC), have been shown to play a critical role in the learning of stimulus-reward associations. In non-human primates, populations of neurons in the mPFC have been shown to respond to stimuli or actions as a function of reward expectation (Amiez et al., 2006) and encode for RPEs (Kennerley et al., 2011). In humans, EEG signals originating in the mPFC are modulated by the degree of discrepancy between expected and real outcomes (Cavanagh et al., 2012; Chase et al., 2011; Mas-Herrero and Marco-Pallarés, 2014; Oliveira et al., 2007). In the context of reward, electrophysiological and blood oxygenation level dependent (BOLD) activity in the mPFC have been shown to signal reward prediction at cue and prediction errors at feedback (Silvetti et al., 2014; Talmi et al., 2013; Vassena, Krebs, et al., 2014), as well as correlate with degree of learning of stimulus-reward associations (Mas-Herrero and Marco-Pallarés, 2014). Taken together, these findings suggest that the VS and mPFC/ACC play crucial roles in outcome and reward prediction, both functions that subserve reward-related behavioral adaptation.

However, one critical observation is that the neural substrates that underpin reward learning are also recruited for signaling the subjective value of effort-based rewards. Activity in the VS has been shown to scale positively with the subjective value of rewards across different reward domains and phases of reward processing (Bartra et al., 2013; Mas-Herrero et al., 2021; Sescousse et al., 2013). Furthermore, disruptions to striatal dopamine have been consistently shown to alter preferences for effort-based rewards (Assadi et al., 2009; Salamone et al., 2009; Salamone et al., 2012). With regard to cortical structures, neural substrates within the mPFC appear to be functionally specialized, such that the vmPFC codes reward features (i.e. subjective value) of reward stimuli at both cue and outcome (Bartra et al., 2013; Lopez-Gamundi et al., 2021; Sescousse et al., 2013; Vassena, Krebs, et al., 2014), while the ACC is more associated with option comparison and decision value at cue (Hogan et al., 2019; Shenhav et al., 2014; Westbrook et al., 2019), and prediction error coding and performance monitoring at feedback (Jessup et al., 2010; Silvetti et al., 2013; Vassena, Krebs, et al., 2014). With respect to predicted rewards, BOLD activity in the ACC has been repeatedly shown to scale positively with increasing effort demands and negatively with subjective value (Chong et al., 2017; Klein-Flugge et al., 2016; Prévost et al., 2010). Furthermore, the relationship of the ACC with expected subjective value appears to be specific to rewards with effort costs, but not delay or probability costs (Bailey et al., 2016). Thus, it appears that the VS and mPFC/ACC are also key nodes in representing reward value alongside the effort costs required to obtain them.

Critically, effort itself is a strong reinforcer (Palidis and Gribble, 2020; Skvortsova et al., 2017; Skvortsova et al., 2014) and effort and reward prediction errors have been shown to originate in the dopaminergic midbrain but project to functionally distinct regions (Hauser et al., 2017). Moreover, RPEs are modulated by the subjective value or utility of rewards (Lak et al., 2014; Roesch et al., 2007; Schultz et al., 2015; Stauffer et al., 2014) and have been shown to be sensitive to effort costs required to obtain them (Jarvis et al., 2022; S. Tanaka et al., 2019). In non-human primates, it has been shown that cue-reward contingencies are acquired more quickly when rewards are earned by exerting more, as opposed to less, cognitive effort. However, in this paradigm, reward rates between high and low effort conditions were controlled by randomly aborting some low effort trials (S. Tanaka et al., 2019). Thus, it is unclear if cue-reward contingencies were learned more quickly under high effort because rewards were more valued or because rewards were more certain than those in the low effort condition. Furthermore, the few studies that have tested the effect of effort in the context of reinforcement learning have limited their analyses to cases where effort expenditure was successfully executed (Jarvis et al., 2022; S. Tanaka et al., 2019). Since several of the brain regions involved in reward and effort prediction are also implicated in performance monitoring functions (Drueke et al., 2015; Ferdinand and Opitz, 2014; Luft et al., 2013; Ullsperger and von Cramon, 2003; Vassena, Krebs, et al., 2014), it would be of key interest to understand how reward predictive cues are updated in the context of failure as well as success.

Here, we seek to fill this gap by studying how cognitive effort demands modulate reward learning in humans. To this aim we designed a behavioral paradigm where stimulus-reward contingencies were learned only though experience and reward feedback was received only after completing a cognitively effortful task. Due to the exploratory nature of this study, we had two opposing hypotheses. On one hand, there is growing body of evidence which suggests that paid cost increases the saliency and/or value of rewards (Inzlicht et al., 2018). This is in line with our results from Chapter 4, where more attentional resources were allocated to rewards received under greater effort costs. Following this *potentiation hypothesis*, we predict that stimulus-reward contingencies will be learned more quickly when rewards require greater effort to attain, as has been found in previous studies (Jarvis et al., 2022; S. Tanaka et al., 2019). However, the traditional neuroeconomic framework posits that effort costs discount the value of rewards, as evidenced by decreased preference and dampened brain activity for rewards with higher effort costs (Westbrook and Braver, 2015; Zald and Treadway, 2017). Thus, based on the *discounting hypothesis*, we would expect that rewards received under high effort would have lower subjective values and be less reinforcing than rewards received under low effort. Finally, it is possible that effort performance feedback modulates the effect of effort on reward prediction updating, however due to the lack of studies investigating this effect, our hypothesis remains open.

5.3 Methods

5.3.1 Participants and Procedure

32 adults were recruited through the University of Barcelona SONA systems subject pool. Participants were required to be 1) between the ages of 18 and 45, 2) have normal or corrected-to-normal vision, 3) have no current diagnosis or treatment for a psychological condition and

4) not currently receiving treatment for a chronic illness. Participants completed a brief video call with the research assistant to review the informed consent and give instructions for compensation procedures. Participants were paid 5€ for completing the task and could earn up to an additional 4€ based on task performance. Two participants were excluded based on effort task performance that suggested inattention to the overall task (<60% accuracy on effort trials). Participants with extremely little variance in responses to reward cue stimuli (selecting the same cue regardless of reward cue in over >90% of trials) were also excluded (N=2). All remaining participants scored well above chance on attention checks (M=98.2%, SD= 4.5). Three participants were identified as having low model fits (pseudo-R^2<.104) across both effort levels (see model fitting procedure below). All analyses were then repeated excluding these participants. Results remained quantitatively similar, thus we report findings with all 28 participants (20 females, age: M=23.75, SD=3.62).

5.3.1.1 Effort-Based Reward Learning (ERL) Task

Participants first completed a training session where they practiced the different effort tasks. During the training phase, an effort cue would appear for 1500ms, indicating the demand of the upcoming effort task (high or low effort), followed by another fixation cross (1 second) signaling the start of the effort phase. Next, a series of numbers were presented one at a time on the screen for 6 seconds. Numbers ranged from one to nine, excluding five. If the number was yellow, subjects were instructed to use the number keys (1 and 2) to indicate whether the number was higher or lower than 5. If the number was blue, subjects were instructed to use the number keys to indicate if the number was even or odd. In low effort trials, all numbers were yellow, so judgements were always of the same type. In the high effort trials, number color/judgment type alternated, requiring effortful cognitive set switches (Botvinick, 2007; Lopez-Gamundi and Wardle, 2018). Participants were instructed to answer as quickly and as accurately as possible within the 6-second time frame. After the effort task, a fixation cross was presented for 500 ms and then reward feedback for 1 second. Participants were awarded 2 points for successful trials and 0 points for unsuccessful trials. There were 40 trials (20 high and 20 low effort trials) in the practice session.

Participants were told that there was no fixed number of correct responses required within the 6-second time frame. However, they were warned that too few responses and/or too many errors would result in an unsuccessful trial, and that they would not receive the reward for that trial. Unbeknownst to them, thresholds for correct responses for both high and low effort trials were set by looking at the number of correct responses in a moving window of the previous 5 trials of each type. The number of correct decisions required to successfully complete a trial ("decision thresholds") for each trial type are then calculated by taking correct number of decisions above the lower 20th percentile. This locks success rates between high and low effort trials to about 80%, thereby ensuring reward rates do not differ based on effort demand. However, based on previous pilot tests and a previous experiment, basic response standards were set to ensure that participants are investing at least a bare minimum of effort. Specifically, response thresholds could not drop below 4 and 3 correct responses in the low and high effort task, respectively. Trials with more than two errors in the 6-second time window were counted as unsuccessful. The first five trials of the practice were used to set the initial threshold; after this, decision thresholds were updated using the dynamic calibration method.

Upon finishing the practice, participants started the reward learning portion of the task (see Figure 5.1), which was a modified version of the reversal learning task (Cools et al., 2002) where rewards were contingent on both selecting the correct shape and also successful completion of the effort task. In each trial, participants were given 5 seconds to select between two shape stimuli, which were randomly selected at the beginning of each block. One shape was more rewarding, resulting in 5 points in 75% of trials and in 0 points in 25% trials; the other shape was less rewarding (0 points in 75% of trials, 5 points in 25% of trials). If an option was not made within the 5-second time window, a message telling the participant to choose faster appeared for 1-second and then the trial was terminated. Otherwise, a fixation cross appeared for 500ms followed by the effort phase. As in the practice, the numbers task was executed for 6 seconds and decision thresholds were set by a sliding window of the last 5 trials. Once the effort phase ended, another fixation cross appeared for 500ms followed by performance feedback (1000ms) and reward feedback (1000ms). Performance feedback consisted of a thumbs down for unsuccessful effort tasks and a thumbs up for successful effort tasks. During reward feedback, the previously selected shape stimulus was displayed, along with the points earned in either green or red. If the effort task had been successfully completed, the points were green and were added to the total. If the effort task was unsuccessful, the points were shown in red and were not added to the cumulative total; that is, the points in red represented what the participant would have won had they correctly completed the trial. This reward feedback allowed for learning of the stimulus-reward contingencies even in trials where participants were unsuccessful. There were two effort-based reward learning blocks (one low and one high effort, counterbalanced) with 5 sub-blocks with a randomly jittered length of 12 to 18 trials each, totaling to 75 trials per block. At the start of each sub-block, the shape rule was reversed (referred to here as reversal trials) so that the less rewarding shape stimuli suddenly became the more rewarding stimuli. During the first five trials following the contingency reversal, selecting the previously more rewarding stimulus resulted in no points. Participants were explicitly informed of the existence of two probabilities of winning and losing (75% and 25%, respectively) associated with each stimulus and that this probability would be reversed after some unspecified period. Importantly, participants were explicitly instructed to start choosing the other stimulus alternative only when they were completely sure that the rule had changed. Participants were encouraged to accrue as many points as possible on the task and were reminded that payoff was contingent not only on how accurately they selected the stimuli, but also on how well they performed the numbers game.

5.3.1.2 Self-Report Task Ratings

During the ERL task, participants were probed, via 11-point Likert scales, for effort cue liking, reward cue liking, task difficulty, and perceived success rate. At the beginning of the task, participants were instructed to rate the degree they liked the effort cues from the practice and the shape stimuli that would be used in the reversal learning task (0= did not like at all, 5= indifferent, 10= liked very much). After the practice, they were again probed for effort cue liking, but also asked how effortful the High Effort and Low Effort tasks were (0=No Effort, 10=Extreme Effort) and how likely they were to complete each task (0-100%). At the end of each effort-based reversal learning block, participants were probed for their difficulty ratings, perceived success rate, and for how much they liked the shape stimuli used in that block (0= did not like at all, 5= indifferent, 10= liked very much).

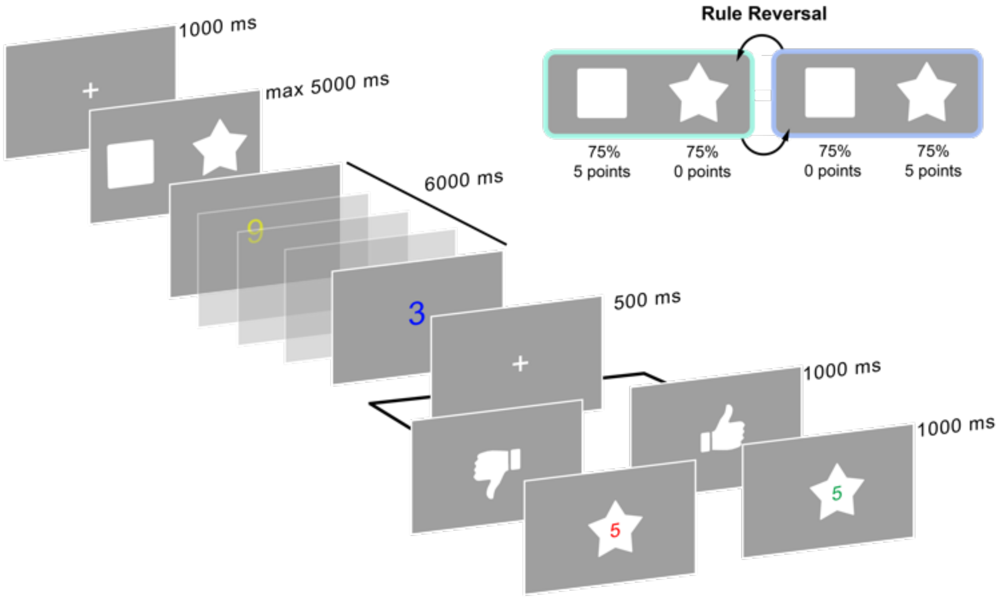


Figure 5.1: Schematic of ERL task. Participants had 5 seconds to choose between the two reward cues. Once selected, the 6-second effort exertion phase began. The degree of effort depended on whether the block was a high or low effort block. After a 500 ms fixation cross, participants received performance feedback followed by reward feedback. Reward feedback, regardless of the magnitude (5 or 0 points) was in green if the participant had correctly completed the effort trial. Conversely, reward feedback was presented in red following negative performance feedback.

5.3.2 Data Analysis

5.3.3 Statistical Analyses

First, we examined if our paradigm effectively manipulated effort demand. Paired samples t-tests were performed to compare the average number of decisions made and the average reaction time for choices in the high effort and low effort numbers task. Self-report ratings of task effort and perceived probability of success were modelled using linear mixed models (LMMs), with effort, task block (baseline vs. task), and their interaction as fixed effects and participant as a random effect. The task was designed so that participants would have an equal probability of correctly completing the high and low effort tasks. However, due to the nature of the task, we also expected that the order of effort blocks could influence success rates. Thus, we used an LMM with effort as a fixed within-subject effect, block order as a fixed between-subjects effect, and participant as a random effect to predict average success rate. Success rates for high and low effort trials on the training were included as a covariate to control for any practice effect.

Next, we analyzed several behavioral events to quantify the degree to which stimulus-reward associations were acquired and if they were preserved. Specifically, individuals who learn the rule quickly should commit a behavioral switch following incorrect negative feedback (negative feedback with the current incorrect action) relatively few trials after a rule reversal. Conversely, once an association is acquired, individuals should shift to a different behavioral policy only when they believe that a rule reversal is likely. Thus, spurious negative feedback should result in more loss-shift errors, or switches to the other, incorrect stimuli, only when participants are expecting a rule reversal (i.e., towards the end of a sub-block). To this end, we computed probability of a behavioral switch following both incorrect negative feedback and spurious negative feedback in the first half (1th to 7th trial) and second half (8th to 18th trial) of the sub-blocks. Probability of behavioral switch as a result of incorrect negative feedback and spurious negative feedback was then assessed via LMMs, with Effort, Block Half, their interaction as fixed effects, and participant as a random effect. Additionally, if participants were learning cue-reward associations, they should be sensitive to previous reward feedback and more likely to make a correct cue choice in later trials (i.e., after receiving more feedbacks after a rule reversal) than in earlier trials. We used a binomial generalized linear mixed effects model (GLMM) with a logit link function to model the dichotomous variable of cue choice (cue with high reward probability vs. cue with low reward probability) as a function of number of trials after reversal, effort, their interaction, and reward feedback on previous trial as fixed effects and participant as a random effect.

Because responses to performance feedback have been shown to be associated with individual differences in learning (Luft et al., 2013), we were also interested in exploring if correct selection of reward cues was influenced by performance feedback on the previous trial. Thus, we used a GLMM to model cue choice as a function of the fixed effects of performance feedback on previous trial, reward feedback from previous trials, as well as their interactions, and including participant as a random effect. Effort demand and trial number were also included as fixed effects. Categorical variables were contrast coded and continuous variables were mean centered and scaled for all analyses.

5.3.3.1 RL Model

We quantified the reward choice data using a Rescorla-Wagner learning rule (Rescorla and Wagner, 1972; Sutton and Barto, 1998; Watkins and Dayan, 1992). Specifically, the stimulus value W(t) for the selected choice were updated as follows:

$$W(t+1) = W(t) + \alpha \cdot (R(t) - W(t))$$

where α indicates the learning rate (constrained between 0 and 1) and R(t) indicates the reward amount (1: reward, 0: no reward) at trial t. In our paradigm, reward feedback was given on every trial, but rewards were only delivered on successful effort trials. Thus, we expected that reward information after a positive performance feedback would be more salient than reward information received after negative performance feedback, since these rewards would be hypothetical. To better capture individual differences in weighing of reward feedback received under the two feedback conditions, we used a dual learning rate reinforcement model (Collins and Frank, 2014; Garrett and Daw, 2020) with two learning rates: α^+ and α^-. This model allows updates to occur differently based on the performance outcome on the effort task. Specifically, updates to the stimulus value W(t) apply α^+ if positive performance feedback was received on trial t and apply α^- if a given trial was not successfully completed. Models were fit independently to the data for high and low effort blocks such that there were two separate learning rates for high (α^+_H, α^-_H) and low (α^+_L, α^-_L) effort. Softmax action selection was used to compute the probability of choosing one of the following two stimuli (A or B):

$$P_A(t) = \frac{e^{\beta W} \cdot A(t)}{e^{\beta W} \cdot A(t) + e^{\beta W} \cdot B(t)}$$

where β is the inverse temperature parameter. β was constrained from 0 to 100 and determines the degree to which choices are made in a more deterministic or stochastic manner. The model was run 10 times, using random initial values for each subject by maximizing the log likelihood estimate with the *fmincon* function of MATLAB R2021. The parameters α and β with the best log likelihood estimate were selected.

Once identified, we used LMM to identify if any variables of interest accounted for differences in learning rate or inverse temperature parameter estimates. Specifically, we used LMM to model learning rate and as a function of the within-subject fixed effect of effort demand and performance feedback, between-subject fixed effect of block order, and participant as a random effect. Within-subject task success rates we also included as fixed covariates to control for performance-related differences in reward rates. Inverse temperature β estimates were log-transformed to correct for right-skewness. These values were then also modeled with an LMM of the same structure as that used for learning rates, except performance feedback was dropped as a fixed effect since inverse temperature parameters were not calculated on the basis of successful vs unsuccessful effort expenditure.

5.4 Results

High Effort Task is More Cognitively Demanding than Low Effort Task. For effort demand to be effectively manipulated in the ERL task, the high effort condition must be objectively and subjectively more difficult than the low effort condition. The data suggests that participants made significantly more choices in the low effort task (M= 7.64, SD=0.85) than on the high effort task (M=5.49, SD=0.77; $t(27)=20.81$, $p<0.001$). Response times were also significantly faster for low effort numbers task (M= 0.56, SD=0.10) compared to high effort trials (M=0.85, SD=0.16; $t(27)=-15.21$, $p<0.001$), which suggests that decisions in the high effort task were more cognitively demanding than those in the low effort task. Self-report data revealed that participants also rated the high effort task (M=7.54, SD=1.58) as more effortful than the low effort task (M=4.95, SD=2.50; $b=1.30$, $p<0.001$) overall. However, there was a significant interaction of effort and task block ($b=0.67$, $p=0.008$) such that the low, but not the high, effort task was rated as more effortful after completing the task block than compared to baseline.

The task was designed so that participants would have an equal probability of correctly completing the high and low effort tasks. However, due to the nature of the task, we also expected that the order of effort blocks, as well as efficacy in the training sessions, could influence success rates. In line with previous results from this task, overall accuracy rates on the effort task were about 75% on each block (Low Effort: M=75.8%, SD=2.9; High Effort: M=72.5%, SD=4.2). LMM models revealed that effort demand indeed had a significant effect on success rates (b=-0.016, $p=0.005$), suggesting that participants were less likely to successfully complete high effort trials despite our dynamic calibration mechanism. On average, participants had 5%

(SD=8.7%) difference in success rate between low and high effort blocks. These differences were not driven by order effects (*b*= -0.009, *p*=0.152) or success rates during the training session (*b*= 0.021, *p*=0.774) but, since learning rates have been shown to be sensitive to outcome probability, we included block success rates as covariates in all relevant analyses.

Successful Learning of Cue-Reward Associations. Choice behavior suggests that participants' choices were sensitive to rule reversals. Participants presented, on average, a cue selection accuracy rate (proportion of correctly selecting the more rewarding cue divided by the total number of choices) of 77.7% (SD=6.4%) and earned 7.85€(SD=0.44). If participants were learning the structure of the task, they should be more likely to switch from the current correct response to the current incorrect response following a spurious negative feedback towards the end of the block, when reversals are more likely. As expected, we detected a significant effect of block half (*b*=0.015, *p*<0.001) on loss-shift error rate, such that individuals switched more following a spurious negative feedback at the end of the block (M=0.11, SD=0.05) than at the beginning of the block (M=0.07, SD=0.05). However, we did not detect any significant effect of effort (*b*= -0.003, *p*=0.330) or the interaction of effort and block half (*b*=0.002, *p*=0.596), which suggests that loss-shift error rates were not affected by effort demands (see Figure 5.2A). Similarly, participants should be more likely to switch following negative feedback with the current incorrect action at the beginning of the block, when a reversal recently occurred, compared to the end of the block once the rule has been acquired. Again, as expected, we found a significant effect of block half (*b*= 0.015, *p*<0.001), such that participants made correct behavioral switches more frequently at the beginning (M=0.19, SD=0.06) compared to the end (M=0.16, SD=0.06) of the block (see Figure 5.2B). The effect of effort (*b*= -0.006, *p*=0.156) and the effort-block half interaction (*b*= -0.002, *p*=0.690) were not significant.

If participants were learning cue-reward associations, they should be increasingly likely to select the correct reward cue as they receive more feedback after a rule reversal. As seen in Figure 5.2C, the odds of selecting the correct reward cue increased as a function of number of trials after reversal (*b*=0.165, *p*=0.004) and previous correct reward feedback (*b*=0.687, *p*<0.001). However, we did not detect a significant effect of effort demand (*b*= -0.056, *p*=0.441) or interaction between effort and trial (*b*=0.013, *p*=0.821) on probability of selecting the correct cue, suggesting that learning occurred but was not clearly modulated effort demand. Finally, if participants understood the relationship between cues and rewards, they should not develop an overall preference for a cue since the cue-reward association switches over the course of the task. In line with this theory, we found no significant effect of task block (*b*= -0.142, *p*=0.230) or cue shape on self-report ratings of cue liking. Furthermore, we found no effect of effort, or significant interactions (all *p's*>0.230), suggesting that self-report cue ratings did not differ significantly from baseline and were not modulated by effort demands or simple preference for a cue image. Finally, we expected that delivered rewards (rewards presented after positive performance feedback) would be more salient than undelivered rewards (after negative feedback), and that this may impact cue selection. Thus, we tested the effect that effort performance outcomes had on probability of selecting the more rewarding cue. GLMM revealed a significant effect of previous reward outcome, such that negative reward feedback on the previous trial increased the odds of correctly selecting the correct cue on the current trial. As expected, GLMM also detected a significant main effect of previous performance feedback (*b*=0.619, *p*<0.001) and

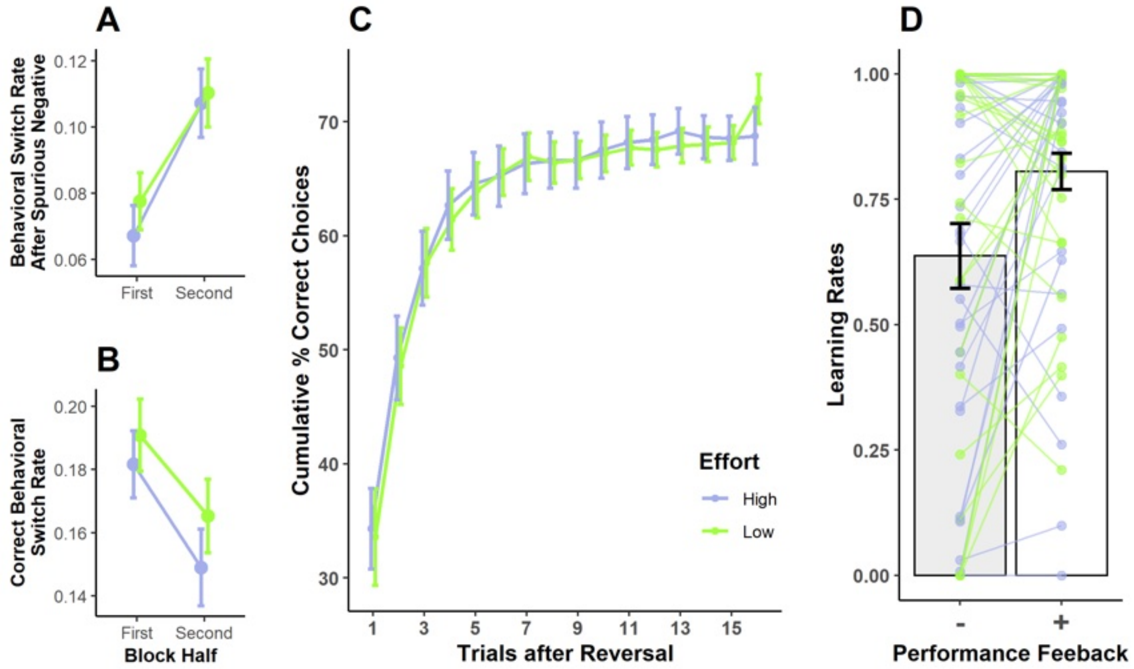


Figure 5.2: Results for ERL Task. **A)** The average rate of behavioral switches after receiving a spurious negative feedback. Participants were less likely switch to the less rewarding cue after receiving a spurious negative feedback in the beginning of a sub-block, but were more likely to switch at the end of the sub-block in anticipation of a rule reversal. **B)** The average rate of switching to the more rewarding cue in response to a negative feedback from the less rewarding cue. Participants were more likely to switch to the more rewarding cue at the beginning of the sub-block when they are acquiring a new rule compared to the end of a sub-block. **C)** The average cumulative percentage of high-reward cue choices after a rule reversal. By the third trial, subjects were generally discriminating between cues at above chance level. Points represent sample means and error bars represent the standard error. **D)** The effect of performance feedback on learning rates. Positive and negative signs on the x-axis signify positive and negative performance feedback, respectively. Overall, participants had higher αestimates for positive performance feedback. Lines connect each participants α^+ and α^- estimates for high and low effort.

previous performance and reward feedback interaction (b=1.843, p<0.001), such that successful completion of the effort task increased the odds of selecting the more rewarding cue, especially when previous reward outcomes were positive. No significant effect of effort demand (b=-0.057, p=0.506) was detected.

Learning Rates Modulated by Performance Feedback, but Not Effort. In order to formalize the impact of performance feedback and effort demand on the learning of cue-reward associations, we fit participants' choices to a dual learning rate model where reward predictions were adjusted on the bases of both effort demand and performance feedback (High Effort pseudo-R^2: M=0.35, SD=0.20; Low Effort pseudo-R^2: M=0.33, SD=0.20). Across feedback types, participants had a mean learning rate of 0.69 (SD=0.34) and median inverse temperature value of 2.79 (SD=19.80) on high effort blocks and a mean learning rate of 0.76 (SD=0.32) and median inverse temperature value of 2.25 (SD=25.63) on low effort blocks. Our LMM revealed a significant effect of performance feedback (b=0.084, p<0.001) on learning rate estimates. As shown in Figure 5.2D, learning rates were higher after positive (M=0.806, SD=0.261) compared to negative (M=0.637, SD=0.366) performance feedback. Contrary to our hypothesis, but consistent with the previous behavioral findings, we found no significant effects of effort demand (*b*= -0.043, *p*=0.116) on α estimates. Moreover, we found no significant effect of effort demand and performance feedback interaction (*b*=0.020, *p*=0.402), or average trial accuracy (*b*= -0.364, *p*=0.680). Taken together, these findings suggest that the reward values were updated on the basis of performance feedback, but not effort, even when we controlled for performance-related success rates. Conversely, LMM did not detect any significant effect significant effect of effort (*b*= -0.050, *p*=0.660), block order (*b*= -0.180, *p*= 0.403), or task success rates (*b*= -1.402, *p*=0.705) on estimates of inverse temperature parameter, suggesting that choice selection was not guided by effort demands, order effects, or average performance.

5.5 Discussion

Learning which actions lead to rewarding outcomes is critical to all goal-directed behavior. In the present study we investigated the effect of cognitive effort on shaping reward learning behavior. Our results indicate that cognitive effort demand was effectively manipulated and that participants were able to adapt choice preferences based on shifting values of reward-predicting cues. However, we found no evidence that learning rates were modulated by paid effort costs. Instead, learning rates were modulated by performance feedback, which suggests that reward values are more efficiently updated as a function of successful execution of task – and therefore real attainment of reward – as opposed to unsuccessful execution of task.

In the current study, effort demand was effectively manipulated but did not measurably impact the value of reward-predictive cues. Behaviorally, participants were able to make more choices with faster reaction times in the low effort cued set-switching task. This aligns with subjective reports which indicated that our participants reliably rated the high effort task as more difficult and less likely to successfully complete than the low effort task. However, if rewards had been devalued by increasing effort demands, we would expect that reward-predicting cues in the high effort block would be less subjectively valued than cues in the low effort block. We found no evidence that effort discounted or, alternatively, potentiated the net value of reward. Specifically, participants in our sample did not rate liking reward-predictive cues differently based on the effort demands associated with them. Furthermore, we did not find any effect of effort on learning rate, which implicitly suggests that the subjective value of reward was not sufficiently modulated by effort demands to alter the learning of stimulus-outcome associations. Thus, our findings fail to support both the effort discounting and potentiating hypotheses.

There are several potential explanations for why we did not detect an effect of effort. First, the block nature of the task could make it so that net values of rewards were not being computed based on relative effort costs. Several frameworks have proposed that the net value of an option is computed in service of option comparison (Kolling et al., 2016; D. J. Levy and Glimcher, 2012; Shenhav et al., 2014). Thus, it is plausible that converting rewards into a "common currency" may be irrelevant in contexts where effort demands are locked, as occurs in paradigms where trials of varying effort demands are not interweaved. However, this rationale would not explain findings from other studies that demonstrate neural signals of effort discounting at cue and feedback in studies with block designs (Botvinick et al., 2009; Porter et al., 2019).

Second, it is possible that our paradigm captured the paradoxical effects of effort by separating cue choice from reward feedback. Specifically, choices about reward cues were made before effort exertion while feedback about those choices was received after. Thus, it could be that prospective effort devalues reward at cue when a choice is being made but increases saliency at feedback, when reward is delivered after successful effort expenditure (Inzlicht et al., 2018). If this were the case, we would expect that cue-outcome contingencies would be more efficiently updated for rewards received under greater effort cost, but that this information may not guide later decisions, where prospective effort costs presumably attenuate expected net value of reward-predictive cues. This postulation is partially in line with reports from previous voltammetry (Gan et al., 2009; Wanat et al., 2010) and electrophysiology (Pasquereau and Turner, 2013) studies in animals which found that effort costs guide behavioral preferences but are weakly incorporated into cue-evoked dopamine-associated signals, suggesting a partial dissociation between stored value representations and action selection (Hollon et al., 2014). Further, it is worth noting that the effort-based reward learning paradigm used in Tanaka et al. (2019) required subjects to choose between reward cues only after execution of response costs, thereby eliminating any potential distortions to reward value that could occur when expecting prospective effort costs. This dovetails with recent findings that participants are effort averse during the time of choice, but that increased effort expenditure positively shifts RPEs, suggesting an increased subjective value for rewards received through more effort (Jarvis et al., 2022) Critically, the degree to which effort costs shifted RPEs was related to the degree of effort discounting, such that participants who are more effort averse later allocated more value to rewards gained through more effort (Jarvis et al., 2022), thereby highlighting the dissociation between how effort is represented at choice versus feedback. Future studies will be needed to study the opposing effects of effort on net value and how these effects influence behavioral adaptation to rewards.

Alternatively, one of the strengths of our paradigm was that we orthogonalized the effect of effort expenditure from performance feedback. Our findings indicate that reward values were updated as a function of performance feedback irrespective of effort demands, such that learning rates in our sample were enhanced by positive performance feedback. This finding is in line with the observation that neural activity associated with reward prediction violation is also responsive to performance feedback. For example, the VS, a region critical for reward saliency and prediction signaling (Schultz, 2016), is also sensitive to positive performance feedback (Drueke et al., 2015; Ullsperger and von Cramon, 2003). BOLD activity and EEG signals generated in the ACC are enhanced for unlikely rewards (Hajihosseini and Holroyd, 2013) and scale with unsigned reward prediction error (Mas-Herrero and Marco-Pallarés, 2014), but are also enhanced for unexpected positive (and negative) performance feedback (Ferdinand and Opitz, 2014; Luft et al., 2013; Vassena, Krebs, et al., 2014). Similarly, amplitudes of the component P3, which have been shown to scale with better-than-expected rewards (Glazer et al., 2018; Hajcak et al., 2007), are also larger following correct performance feedback (Kirsch et al., 2022; Luft et al., 2013). Thus, it is plausible that a common network subserves both reward prediction and performance monitoring functions and that rewards received from successful performance are upregulated when informing future action policies.

It is also worth noting that the reward-sensitive component P3, has also been shown to be responsive to the degree to which effortful responses lead to reward (e.g., reward efficacy), such that feedback-evoked P3 tracks the magnitude of unsigned efficacy prediction errors (Grahek et al., 2022). Furthermore, greater control is allocated when task performance is more predictive of reward, as demonstrated by better behavioral performance and enhanced EEG indices of cognitive control (Frömer et al., 2021; Grahek et al., 2022). This is critical when interpreting our findings alongside the results reported in Tanaka et al. (2019). Reward rates in the Tanaka et al. (2019) were equalized between conditions by randomly aborting low effort trials, resulting in lower efficacy in the low effort condition since likelihood of receiving reward on these trials was less contingent on performance than it was on high effort trials. Therefore, it is plausible that cue-reward contingencies in the Tanaka et al. (2019) study were learned more quickly under the high effort condition because effort expenditure was simply more predictive of reward than in the low effort condition. Although we were unable to equalize success rates in the present study, average success rates were controlled for statistically and rewards were wholly contingent on performance, allowing us to rule out any confounding effects between effort demand and reward likelihood and efficacy.

Despite the strengths of our paradigm, there were also several limitations. As mentioned before, success rates were not completely equal between effort conditions. Although we controlled for this statistically and by providing reward feedback even in negative trials, we could not control for prediction errors driven by differences in performance-related reward expectancy. However, due to the block nature of the task, it is unlikely that this contributed to the lack of effort effects since the difference in reward rates between conditions was relatively small could not be estimated on the fly. Second, our sample size was too small to explore personality traits that may moderate the impact of effort on reward. For example, differences in the degree to which individuals find cognitively demanding tasks pleasurable has been shown to impact the subjective weight of effort costs (Viola et al., 2015; Westbrook et al., 2019). Similarly, individual differences in consummatory and anticipatory anhedonia are also linked to behavioral and brain neural correlates of effort discounting and responsiveness to reward feedback (Gradin et al., 2011; Huang et al., 2016; Liu et al., 2014; Padrão et al., 2013; M. T. Treadway et al., 2009). It has also been demonstrated that individual differences in effort discounting directly modulate the effect of effort on RPEs (Jarvis et al., 2022). Thus, it is possible that effort acts as a positive reinforcer for some individuals and a negative reinforcer for others, such that effort-related effects exist but are not detectible when averaged at the group level. The exploration of how individual differences in reward and effort costs sensitivity impact learning aspects of reward processing is critical for future studies in goal-directed behavior.

In conclusion, the present study we developed a new paradigm to investigate the impact of cognitive effort on reward learning behavior. While participants were able to adapt their choice preferences based on shifting values of reward-predicting cues, no evidence was found that learning rates were influenced by paid effort costs. Instead, learning rates were modulated by performance feedback, suggesting that reward values are more efficiently updated based on successful task execution and the attainment of rewards. Many psychopathological conditions, such as schizophrenia (Barch et al., 2014; Cooper et al., 2019; Gradin et al., 2011), depression (Hammar et al., 2011; Liu et al., 2014; M. T. Treadway, Bossaller, et al., 2012; M. T. Treadway et al., 2015), and substance use disorders (Goldstein and Volkow, 2011; Leventhal et al., 2008), are characterized by abnormal reward sensitivity, prediction, and motivation. Although these symptoms frequently occur simultaneously, these different goal-directed processes are oftentimes studied in isolation, making it difficult to understand how these reward features are integrated and altered in different psychopathological conditions. This study provides the first step towards developing a paradigm that can answer these questions.

Chapter 6

Discussion

The three studies presented in this thesis aimed to empirically address how effort demands impact reward value across different phases of reward processing. Primarily, we sought to answer which brain regions consistently signal effort demands and net value of prospective rewards, elucidate the neural mechanisms underlying the assessment of cognitive effort demands during cue evaluation and reward delivery, and examine how effort demands influence the updating of reward-predictive cues. To achieve these goals, a range of methodologies, including fMRI meta-analysis, EEG, and novel behavioral measures, were employed, with careful consideration of controlling for confounding factors. By employing a diverse set of techniques and examining effort and net value across various stages of reward processing, this research provides a comprehensive understanding of how effort cost affects the neural and behavioral representations of reward value while also shedding light on the circumstances under which effort cost is relevant to the representation of net value.

In the following sections, we will discuss the results of these three studies and evaluate to which extent our research aims were accomplished. The theoretical contributions of this thesis to the neuroscience of cost/benefit decision-making will also be discussed, along with the strengths and limitations of the methodologies employed. Furthermore, we will also discuss new research questions that can be derived from our findings and future directions for this field of research, given the current results and obstacles we encountered.

6.1 Research Aims and Experimental Results

As discussed earlier, previous findings suggested that the net value of effort-based rewards may be represented in regions outside of the common valuation network. Motivated by these findings, we aimed to *identify areas consistently involved in effort valuation and net value signaling*. In Study 1, we answered this question by meta-analytically analyzing imaging data from most of the imaging studies exploring cue-related signals of effort-based reward and decision-making. This method permitted us to directly compare data from strikingly diverse effort-based reward paradigms, including tasks with different effort manipulations (i.e., cognitive and physical effort), reward types (i.e., monetary, attractive pictures, etc.), decision-making schema (i.e., no choice, options presented sequentially, two options presented simultaneously, etc.), reward delivery and effort expenditure procedures (i.e., cumulative reward, randomly selected trials, etc.), and net value metrics (i.e., single offer SV, effort-reward interaction, difference in SV, etc.). Furthermore, by using a hybrid image- and coordinate-based approach, we were able to maximize the amount of data included in our analysis, which allowed us to more confidently identify the brain regions that are consistently recruited in signaling prospective effort demands and net value in incentivized effort tasks.

Results from our region-of-interest (ROI) analyses revealed a double dissociation between the pre-SMA and the vmPFC, such that across studies, the pre-SMA was consistently activated for increasing prospective effort costs and deactivated for increased net value. In contrast, the vmPFC showed the opposite effect. ROI analyses also indicated that the VS was uniquely involved in net value signaling, such that the VS was consistently positively activated for net value but not for prospective effort. These findings were confirmed by whole-brain analyses, and overlap with results from previous meta-analyses (Bartra et al., 2013; Clithero and Rangel, 2014). Several meta-analyses have identified the vmPFC and VS as central nodes in representing the subjective value of rewards across reward domains and reward processing phases (Bartra et al., 2013; Clithero and Rangel, 2014; D. J. Levy and Glimcher, 2012; Mas-Herrero et al., 2021; Sescousse et al., 2013). Furthermore, the clusters we identified in the pre-SMA and dACC as positively tracking effort and negatively tracking net value coincide with findings from Bartra et al. (2013), which identified a large cluster in the mPFC that was deactivated in response to increasing subjective value. While the contrasts used in Bartra et al. (2013) were mainly from the outcome phase, the study also included studies with probabilistic outcomes and learning paradigms, as well as a variety of reward domains. Thus, our findings suggest that the pre-SMA/dACC is critical to tracking the subjective values of rewards across a variety of different paradigms and modalities.

ROI findings, however, were only partially supported by supplementary analyses which tested the extent to which our results were robust to different features of effort-based reward paradigms. For example, when studies that used choice difficulty metrics as markers for SV (e.g., SV difference) were removed from the analyses, activation patterns in the VS and vmPFC remained largely the same. However, we no longer detected net value deactivations in the pre-SMA. This result partially supports other reports that the pre-SMA and posterior ACC is recruited primarily for comparison between close alternatives, while the vmPFC seems to be more reliably recruited for SV encoding, especially for single offers (Hogan et al., 2019; Shenhav et al., 2014; Westbrook et al., 2019). Furthermore, when studies with cognitive effort were removed from the analysis, we no longer detected a consistent effect of prospective effort in the vmPFC, and we found a very unreliable effect of the dACC/pre-SMA in signaling net value, which partially supports the idea that certain domain-dependent regions are recruited for specific types of effort demands (Schmidt et al., 2012). Finally, we conducted another supplementary analysis which only included studies where effort requirements were certain and executed online during scanning. This analysis replicated findings that BOLD activity in the bilateral pre-SMA and ACC was positively associated with effort demand but failed to detect a negative association between raw effort and activity in the vmPFC.

Taken together, we can reach two conclusions from this study. First, the pre-SMA and dACC robustly and consistently signaled raw prospective effort while the vmPFC and bilateral VS robustly and consistently signaled net value. Second, although supplementary analyses lacked sufficient statistical power to fully explore these hypotheses, their findings suggest that the robustness of our effects was partially sensitive to features of the experimental paradigms.

After identifying the dACC/pre-SMA as a central node for encoding prospective effort and net value of effort-based rewards, we were interested in exploring how, in the absence of confounders, mPFC signals of effort and net value evolve over time. Specifically, once we had identified the neural substrates involved in signaling effort-based reward processing, we were also interested in *identifying potentially separable and distinct effort, reward, and net value signals* in the absence of choice and in a context where other confounds, such as differential reward probability between effort conditions, were experimentally controlled. To this end, we designed two novel effort-based reward paradigms that varied cognitive effort demand while holding success rates, and therefore reward rates, constant between effort conditions. Participants completed this task while we recorded scalp EEG. Specifically, we were interested to what degree theta oscillations captured raw effort and net value signals since frontal midline theta (FMT) has been shown to be generated in the midcingulate cortex and pre-SMA, regions which coincide with the clusters identified in Study 1 (Cavanagh and Frank, 2014; Mas-Herrero and Marco-Pallarés, 2016). Cue- and feedback-related component P3 amplitudes were also measured in order to ensure that our effort and reward manipulations were effective and to provide an index of saliency.

Contrary to our hypothesis, FMT power was generally enhanced at cue presentation but was not sensitive to reward magnitude, reward probability, or effort demands, nor did this signal reflect integrated net value. These findings were consistent across both EEG samples. Furthermore, at cue, P3 amplitudes were only sensitive to reward magnitude and probability, but not upcoming effort demands. These findings suggest that in the absence of differential reward rates, upcoming effort demands and net values were not indexed by these two EEG signals. However, effort enhanced reward-related and probability-related P3 amplitudes at feedback. Moreover, FMT power was enhanced for rewards gained under high compared to low effort but was not sensitive to reward magnitude or probability, again suggesting a lack of integrated net value signal. Taken together, these findings reveal that more attentional resources are allocated to reward feedback after high effort expenditure and that the salience of larger or less probable rewards scales positively with increased paid cost.

The finding that more attention and salience is allocated to rewards earned through high compared to low cognitive effort falls in line with several reports that effort costs potentiate, as opposed to attenuate, the value of rewards at feedback. Since reward prediction errors have been shown to be sensitive to the subjective value of reward (Jarvis et al., 2022; Lak et al., 2014; Roesch et al., 2007; Schultz et al., 2015; Stauffer et al., 2014), we decided to explore if the effect of cognitive effort demand on reward value could be captured by *how effort costs alter learning of cue-reward contingencies.* There were two competing hypotheses. First, since greater attention is being given to high effort outcomes, we hypothesized that the value of reward predictive cues would be updated more efficiently for rewards gained through more effort expenditure, such that individuals would have better learning rates for high effort rewards. Conversely, if effort discounted the value of reward, we would expect that individuals would learn stimulus-reward contingencies less efficiently for rewards with higher effort requirements, since these rewards are deemed less subjectively valuable. To test these competing hypotheses, we designed a novel behavioral paradigm where participants had to learn cue-reward associations through experience but could only obtain said rewards by successfully executing a high or low cognitive effort task. Results revealed that participants were able to learn cue-reward associations but that the rate of learning was not modulated by cognitive effort demand. Instead, we found that learning rates were sensitive to performance feedback, such that the value of reward-predictive cues were more accurately updated after successful effort outcomes. Thus, while we were not able to replicate previous results showing that learning speeds in non-human primates were higher when there was a higher cost required to obtain a reward (S. Tanaka et al., 2019), we provide a variety of suggestions of why differences between our adapted paradigm and the one used in animal research yielded different results.

Overall, the empirical results of this thesis suggest that effort costs are represented differently across the stages of reward processing. The majority of the studies used in Study 1 involved choices between high effort/high reward options and less effortful/less rewarding options, thereby subjective value was generally observable through behavioral data. Here, we detected neural regions whose activation patterns correlated with classic effort discounting accounts (i.e., scaled positively with subjective value and negatively with effort demands – and vice versa). While in Study 2 we failed to detect these net value signals during the cue phase, we saw that effort indeed enhanced the saliency of received rewards. These findings partially fall in line with other reports that more value is allocated to rewards earned through effort (Inzlicht et al., 2018). However, since salience is distinct from net value (Kahnt and Tobler, 2017), a more conservative interpretation of our findings would be that rewards received via high effort costs are attended to more, and that paid cost has an additive effect on the salience of high magnitude and unlikely rewards. Finally, in Study 3, performance feedback, but not effort demands, modulated reward learning, suggesting that effort demands are not relevant when updating the value of reward-predictive cues in a context where reward receipt depends more on general performance and selection of stimuli than on demand-driven differences in success rate.

6.1.1 Theoretical Implications

6.1.1.1 Common valuation network only partially involved in effort valuation

The activation patterns in the vmPFC identified in Study 1 are consistent with integrated cost/benefit signaling specifically for effort-based rewards. As part of the common valuation network, meta-analytic results have shown that activity in the vmPFC consistently reflects not only the subjective value of rewards across reward processing phases and incentive types, but also for different cost requirements associated with said reward (Bartra et al., 2013; Clithero and Rangel, 2014; D. J. Levy and Glimcher, 2012; Mas-Herrero et al., 2021; Sescousse et al., 2013). However, the same activation pattern was not detected for the VS, which is also considered to be a central node of the common valuation network. In our meta-analysis, VS activity correlated exclusively with net value and did not reliably scale with prospective effort costs. This finding is surprising given the substantial evidence showing that VS regulates effort-based decision-making behavior via modulation of effort cost weighting (Salamone et al., 2001; Salamone and Correa, 2012; Salamone et al., 2018; Salamone et al., 2016) and that VS activity signals prospective effort costs (Croxson et al., 2009; Kurniawan et al., 2013; Schmidt et al., 2012; Schouppe et al., 2014).

One plausible explanation could be that the striatum holds both effort activation and effort-discounted net value representations, but the opposing nature of these signals hampers detection, as demonstrated by Suzuki et al., (2021). This interpretation is consistent with meta-analytic findings which demonstrated that striatal activations associated with subjective value at cue were primarily accounted for by studies that used the Monetary Incentive Delay Tasks, a paradigm which requires an incentivized response at cue (Bartra et al., 2013). Furthermore, while it is possible that these opposing signals cancel each other out completely, it is also plausible that they are weighed asymmetrically, resulting in detection of one signal but not the other. Specifically, in a paradigm where effort-based valuation was isolated from production demands and outcome resolution, BOLD activity in the vmPFC tracked both prospective effort costs and discounted net value during choice, while the VS only tracked net value (Aridan et al., 2019). Thus, in our meta-analysis, it is possible that these conflicting signals obscured detection of effort cost signal, but not activity related to net value. However, this would not explain why supplementary meta-analyses did not reveal any consistent effort-related signaling in the VS when analyses were limited only to studies with online effort exertion, a condition where we would assume invigoration functions of the VS would be more present ("Action controls dopaminergic enhancement of reward representations.", 2012).

Alternatively, it could be that VS receives effort and motor demand input from other regions and integrates this with reward value and reward rate input from the SN/VTA (Viviani et al., 2020) to generate net value signals. For example, the VS may receive effort input from more dorsal regions of the striatum, which has been shown to track effort costs ("Action controls dopaminergic enhancement of reward representations.", 2012; Burke et al., 2013; hua Yang et al., 2016; Klein-Flugge et al., 2016; Kurniawan et al., 2010; Kurniawan et al., 2013), and integrate this with reward value inputs from the SN/VTA to generate net value signals. However, this hypothesis seems unlikely since dorsal regions of the striatum have also been shown to track the net value of effortful rewards (Klein-Flugge et al., 2016; Seaman et al., 2018) and results from Study 1 identified consistent net value, but not raw effort cost, signaling in the DS, even in motor-related areas of the striatum, such as the putamen.

Another alternative is that the VS receives information about raw effort demands from more cortical regions and incorporates this information into a net value signal. The basal ganglia has strong connections with cortical structures that are key for subjective value representation, such as the OFC and vmPFC, as well as regions more involved in cognitive control and motor functions, such as the SMA, pre-SMA, and cingulate cortex (Isaacs et al., 2018). With regard to incentive effort task, it has been shown that activity in the dACC during cognitive effort exertion was related to the feedback-related subjective value signal in the nucleus accumbens (Botvinick et al., 2009). However, interpretation of this finding is complicated by the fact that reward outcomes were randomly generated and not contingent on effort expenditure (Botvinick et al., 2009), thus it remains unclear to what degree VS response at reward delivery was representative of effort-discounted subjective value or reward prediction. By separating effort and reward valuation from effort production or by using methods with higher spatial and temporal resolution (e.g., intracranial recordings), future studies could dissociate the roles of cortical structures, primarily the ACC and vmPFC, and striatal contributions to effort-based decision-making.

6.1.1.2 Coherence with Predominate Frameworks of Incentivized Effort Allocation

Several theories have been proposed to explain how effort and reward drive goal-directed behavior. These accounts generally use reinforcement learning principles and/or cognitive control frameworks to provide mechanistic descriptions of adaptive effortful behavior and implicate the mPFC in various aspects of this process (Vassena, Holroyd, et al., 2017). Although a comprehensive review of these models is outside of the scope of the current work, we will briefly describe some of the predominate theories of reward-related effort-allocation and evaluate how our findings contribute to these theories.

One of the first unifying accounts of the role of the mPFC in signaling response-outcome predictions in the service of goal-directed behavior was the predicted-response outcome (PRO) model (Alexander and Brown, 2010, 2011). Specifically, the PRO model suggests that the mPFC uses reinforcement learning systems to support the motivation of extended, effortful behaviors. By this account, the mPFC simultaneously monitors multiple potential outcomes and generates signals to update response outcome predictions. These signals take the form of prediction errors which represent surprising events, such as "unexpected occurrence and "unexpected non-occurrences" as opposed to reward expectancy violations per se (Alexander and Brown, 2010; Vassena, Holroyd, et al., 2017). Thus, in contexts where errors are the more likely outcome, the PRO model would predict that mPFC activity would be enhanced for positive outcomes since these outcomes are more surprising (Alexander and Brown, 2019; Vassena et al., 2020).

In the second experiment of Study 2, success rates were at about 50% in the low probability condition and about 85% in the high probability condition. Thus, it follows that under the PRO model, oscillatory activity generated in the mPFC, such as frontal midline theta, would be enhanced for successful low probability trials compared to high probability trials. Yet, we found no probability-related differences in FMT power at outcome. It is worth noting, however, that participants in Study 2 were explicitly told which cues indicated lower probability of success. Therefore, it is possible that although trial success was unlikely in the low probability condition, the mPFC did not register this outcome as surprising since reward probabilities were explicitly described at the beginning of the task. Conversely, participants were not told that probability of success was independent of effort demands. Thus, it is possible that in our paradigm, the mPFC relied more on information about effort performance to shape outcome expectancies. This would result in enhanced theta power for rewards received under high effort, but also for failure to receive reward in low effort trials, a condition which we were not able to analyze in the current study.

The PRO framework was later extended to encompass effort-based behavior using hierarchical error representation (HER; Alexander and Brown, 2015). Like the PRO model, the HER (or PRO-effort) model also posits that the mPFC tracks outcome-related information (such as effort and reward) via predictions and violations (Alexander and Brown, 2015; Vassena, Deraeve, et al., 2017). However, this model additionally provides a mechanistic understanding of how changing environmental information might affect decision-making and task performance in effort-based choices (Vassena, Deraeve, et al., 2017, 2020). In the context of effort-based decision-making, the mPFC monitors prospective reward and effort (via cues and outcomes) with the same mechanisms used to monitor the occurrence of any other stimulus and response outcome. However, the HER model does not propose that effort costs are computed directly in the mPFC, nor does it suggest that the mPFC necessarily drives decisions to engage in a proposed task or, once engaged, to maintain performance levels sufficient to achieve successful completion of a task (Vassena, Deraeve, et al., 2017; Vassena, Holroyd, et al., 2017). Rather, signals generated by mPFC are incorporated into decision processes occurring outside of the mPFC/ACC, such as the dorsolateral PFC and basal ganglia (Brown and Alexander, 2017).

Under this framework, we would expect that mPFC activity increases as a function of increased effort requirements while also tracking relevant environmental variables, reflected by net value. This hypothesis is in line with our findings from Study 1. However, the lack of FMT power activity related to reward prediction in the cue valuation phase of Study 2 would appear to contradict this interpretation. Alternatively, under this framework, we would also expect mPFC activity to be sensitive to surprise at cue and scale with the absolute deviation of current reward offer from overall average reward (Vassena et al., 2020). The static reward environment used in our paradigms was not suited to generate surprise signals in FMT, thus, this hypothesis could not be directly tested.

Although both the PRO and HER models rely on reinforcement learning mechanisms to update the value of effort-based rewards, it is unclear what quantitative predictions these models would make regarding to the effort reward learning paradigm used in Study 3. For example, it seems reasonable to predict that mPFC activity during choice would be sensitive to effort and reward predictions based on previous feedback. However, we would expect that feedback-locked mPFC activity should be highest for surprising outcomes, such as negative performance outcomes after the calibration mechanism increased decision thresholds, or spurious negative feedback after stimulus-outcome associations were acquired. Combining neuroimaging with this new effort-reward learning paradigm would allow researchers to more clearly disentangle how effort demands are incorporated into surprise signals.

The PRO and HER models overlap greatly with another neurocomputational account by Holroyd and Yeung (2012) that posits that the ACC not only monitors predictions and outcomes, but is also responsible for selection and maintenance of coherent goal-directed behaviors over extended periods of time (HRL-ACC model). This framework relies on hierarchical reinforcement learning mechanisms and the actor-critic computational architecture to model these behaviors (Cohen and Frank, 2009). Under this framework, the ACC is charged with selecting an action policy. The actor, which is implemented by the dorsal striatum and dorsolateral PFC, then performs the individual actions required to carry out the task, while the critic, which is implemented by the orbital frontal cortex and ventral striatum, monitors those actions by computing the value of ongoing events and prediction errors (Holroyd and McClure, 2015; Holroyd and Yeung, 2012). Phasic dopamine encodes these signals and then utilizes principles of reinforcement learning to adjust and optimize performance on the task (actor) and to optimize reward predictions (critic) (Holroyd and Umemoto, 2016). This model relies on three key assumptions: 1) the actor is effort averse, 2) the ACC control signal attenuates costs so that the actor can generate the behaviors to execute the task, and 3) the level of control is initially high during the early stages of task execution but gradually diminishes to a minimum level required to maintain the reward rate (Holroyd and Umemoto, 2016).

According to the HRL-ACC model, FMT should index ACC control output, and this control signal should attenuate effort costs and be sensitive to reward rate. This theory may explain some of the effects observed in cue theta in the first block Experiment 1 in Study 2. Specifically, we detected enhanced theta power for high effort/high reward cues in the first block (unreported), where success rates (and therefore reward rates) between high and low effort trials remained unequal. Once we removed this block, we no longer detected differences in theta power. Thus, it could be that cue-related FMT power in Study 2 was initially higher for high effort tasks because more control was needed to maintain a high reward rate, but this difference diminished later on once reward rates were equal between effort conditions and minimal control was necessary to support adequate task performance. In addition to effort-driven effects of FMT, this framework would also predict general task-wide variations in cognitive control allocation, as indexed by FMT. For example, in a cognitive effort task that had a duration similar to the tasks used in Study 2, Umemoto et al. (2019) observed that FMT power was characterized by an early phase in which enhanced control levels fostered improved task performance, and a later phase in which enhanced FMT power was also needed to maintain stable task performance, potentially combating reduced valuation of rewards and mental fatigue (Umemoto et al., 2019). Imaging techniques that can capture subcortical activity would be needed to fully test the actor-critic architecture of the HRL-ACC theory and to comprehensively examine how control allocation varies throughout the course of a task.

Another theory that explains effort allocation through the framework of reinforcement learning is the adaptive effort allocation model (Verguts et al., 2015). In this model, the mPFC/ACC plays the dual role of evaluating the potential benefits of expending effort and signaling potential rewarding outcomes. However, this model explicitly modulates effort through a mechanism called ”boosting.” Verguts and colleagues (2015) propose that the mPFC/ACC computes the value of energizing and exerting effort in order to successfully execute an action; this value is referred to as “boosting”. However, exerting effort (boosting) comes with an intrinsic cost, such that an individual will only choose the more effortful option if the value of boosting outweighs the cost (Verguts, 2017; Verguts et al., 2015). Reward and cost feedback is used for learning stimulus-action mapping (via the motor loop) and choosing when and whether to invest effort (via the limbic loop).

Following this theory, mPFC activity will be generally higher for larger rewards, increase with task difficulty as long as the reward justifies the effort, and decrease for tasks that are too challenging to be successfully completed (Vassena, Holroyd, et al., 2017; Verguts et al., 2015). Assuming that all experimental effort tasks were deemed feasible, this model would predict more ACC activation for options with high reward and low cost, consistent with a typical discounting model. However, in Study 1 we found that ACC activity decreases with increasing subjective value. Conversely, the model also explicitly predicts that when task difficulty is low-to-moderate, ACC is more active for (moderately) difficult than for easy tasks. This prediction is in line with the activity detected in Study 1 where ACC activity consistently scaled positively with increasing effort demands. However, FMT power in Study 2 did not display a pattern consistent with a traditional boosting signal. It is also worth noting that Verguts et al. (2015) also described task difficulty as a modulation in accuracy, not solely effort demand. Although the authors did not explicitly distinguish between these two features of difficulty, it would be of interest to explore how the boosting signal responds to isolated variations in both probability of success and effort demands. In addition to the adaptive effort allocation model, which describes how the cortico-striato-pallido-thalamo-cortical pathway regulates effortful behavior, Verguts (2017) also proposed another model which explains how the mPFC synchronizes theta-gamma oscillatory activity in the service of cognitive control. Although theta-gamma phase coupling was not explored in the current work, it could be a potential avenue for future studies on behavioral adaptation in effort-based reward.

In line with the adaptive effort allocation framework, the expected value of control (EVC) theory posits that the mPFC, particularly the dACC, calculates the value of exerting cognitive control (Shenhav et al., 2013). In order to compute the expected value of control, the dACC integrates a variety of signals, including reward magnitude, reward probability, costs, effort, choice difficulty, efficacy, and so on, to determine the optimal control signal (Grahek et al., 2020; Shenhav et al., 2013; Shenhav et al., 2017). In this framework, dACC activity should directly reflect the intensity of the specified control signal, and this intensity should index the amount of control that was deemed worth the expected reward. This model assumes that exerting control is intrinsically costly but does not specify the exact nature of this cost function. In this context, effort demands can alter the EVC signal in two key ways. First, increased effort demands require a larger control signal since more control will be needed to successfully execute the task. Second, in many cases, one is less likely to successfully complete a more effortful task, and this reduced probability contributes to judgements of difficulty. In Figure 6.1 , we can see how reward incentives and task difficulty, which in this case reflects the joined value of effort demand and probability of completion, affect the EVC curve.

While we could not explicitly test EVC hypotheses in Study 1, the paradigms in Study 2 should have been aptly designed to capture this activity, especially at cue. Specifically, one of the strengths of the paradigm we used in Study 2 was that we fully disentangled separate features of task difficulty by orthogonalizing effort demand from probability of success. However, we saw no pattern of activity in the second study that resembled patterns hypothesized by the EVC. Specifically, we would have expected control signals to be most intense (enhanced FMT power) for cues signaling high effort/high rewards and potentially for high effort/low probability, depending to what degree the reward is deemed worthy of control. Note that these predictions are also sensitive to individual differences in probability distortion and effort weighting, as well as affective states (Grahek et al., 2020), which are measures that we did not include in our study.

Taken together, the findings of the current work partially align with neurocomputational accounts that mPFC holds representations of effort prediction and the expected value of available options. While the different theories elucidate various mechanisms by which the mPFC/ACC tracks effort predictions and uses these expectations to guide effort allocation, several lines of empirical evidence also suggest that the mPFC (and FMT) tracks effort and performance

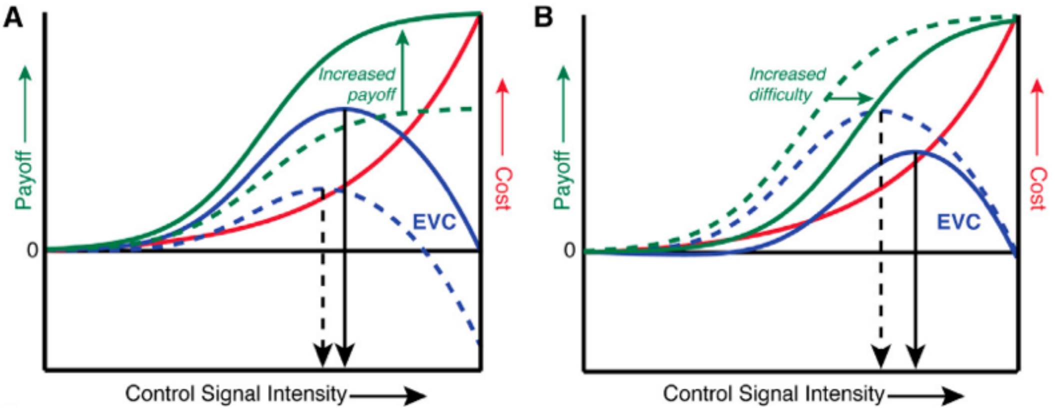


Figure 6.1: Effect of reward (payoffs) and task difficulty on EVC curve and control signal intensity. A) Increasing reward magnitude alters the payoff curve. In this example, monetary reward increases from a low value (dashed green line) to higher value (solid green line). When combined with the cost function (red curve), the EVC curve is altered. As a result, the maximal point of the EVC curve shifts to the right and the control intensity signal increases. **B)** Increasing task difficulty also alters the payoff curve. In this example, task difficulty increases (green dashed line to solid green line) by reducing the probability of success. Combined with the cost function (red curve), this change induces a shift in the EVC function from its initial curve (dashed blue line) to its new shape (solid blue line), As a result, the maximal point of the EVC curve shifts to the right and control intensity signal increases. This figure was adapted from Shenhav et al. (2013).

as opposed to encoding raw effort values. Specifically, it has been argued that the FMT is not an axiomatic RPE signal since its activity does not reflect an interaction between reward and expectancy (Caplin and Dean, 2008; Cavanagh et al., 2012; Hajihosseini and Holroyd, 2013). Instead, FMT is mainly modulated by the unpredictability of events in general and could represent the amount of control needed to obtain a goal of certain subjective value (Holroyd and Umemoto, 2016; E. H. Smith et al., 2015). This is in line with a recent study which reported that the ACC did not correspond to the magnitude of required effort, but in fact reflected a subjective value prediction error comprised of integrated reward and effort cost expectations (Arulpragasam et al., 2018).

This proposal is very consistent with our findings in Study 2, where FMT was insensitive to both reward magnitude and probability at cue and feedback, potentially because reward magnitudes and probabilities were clearly signaled and were almost deterministic. However, the probability of reward based on effort expenditure was not fully deterministic, since effort-related success rates were not explicitly stated and decision thresholds were dynamically adjusted based on current performance and had to be learned through feedback. Therefore, reward feedback —which was also informative of performance feedback —could reflect an updating of future performance predictions, especially under the condition that required more control (high effort). Furthermore, it would explain why effort demands did not modulate learning rates in Study 3, since predictions about effort did not meaningfully influence reward expectancy (i.e., similar success rates between conditions and the block design). Further research is needed to fully elucidate the complex relationship between incentivized effort expenditure and allocation of cognitive control as well as understand how these functions are reflected in mPFC activity and FMT power.

6.1.1.3 Implications for Methodology

Another key focus of the present work has been paradigm development. Specifically, we had three aims: 1) to experimentally disentangle effort demands from reward probability, 2) have rewards be fully contingent on performance and 3) use online effort execution. The first and second aims are critical, since the few effort-based reward paradigms that equalize success rates between effort conditions (Botvinick et al., 2009; Frömer et al., 2021; S. Tanaka et al., 2019) have used methods (e.g. random reward, forced abort, etc.) which reduces the degree to which effort results in reward, which can also impact reward prediction (Grahek et al., 2022). While we were able to successfully accomplish these aims in Study 2, we encountered significant complications when expanding this method to dual-option choice paradigms. Seeing that the few studies that have controlled for probability of success (and reward) have all used passive effort-based reward paradigms (Botvinick et al., 2009; Frömer et al., 2021; S. Tanaka et al., 2019), we believe that these complications merit consideration.

Specifically, we developed and extensively piloted the same cued set-switching task from Study 2 but adapted to the COGED effort-based decision-making paradigm by Westbrook et al. (2013). Before starting the effort-based decision-making portion of the task, participants were required to practice the different levels of effort and make several judgements between a low effort / low reward option and high or medium effort option for a greater reward (see Westbrook et al. (2013, 2019) for details). Critically, these judgements were used to calculate indifference points; low effort reward options for the effort-based decision-making task were then set based on these indifference points according to a proximity parameter (λ), which is a ratio that describes the percent increase (or decrease) of a reward offer relative to the indifference point (Westbrook et al., 2013; Westbrook et al., 2019). Small absolute values of λ indicated that alternatives were close to the indifference point and therefore close in subjective value. Positive values indicated higher subjective value for the low effort / low reward offers, and low effort offers were the same value as their more effortful alternatives when λ=1. Alternatively, negative values indicated higher subjective values for the more costly options, and low effort options were worth 0 points when λ=-1. The purpose of setting reward values with the proximity parameter was to balance choices between high effort and low effort options, as achieved in previous studies (Westbrook and Braver, 2016; Westbrook et al., 2013; Westbrook et al., 2019). Once participants selected one of the two options, they were required to execute the selected cue set-switching task to win the reward. Response requirements were set using the same calibration methods described in Studies 2 and 3, such that participants had equal probability of success across all levels of effort demand. Several versions of the task were tested, with small variations in fixed reward magnitudes, proximity parameters, number of catch trials (trials where λ=-1 or 1) and an average of 108.16 trials (SD=16.13).

Results from the first 87 pilot participants revealed that once probability of success was equalized between conditions, choice patterns were not consistent with effort discounting behavior. For example, Figure 6.2A shows how participants were biased towards selecting the high effort option, even in cases where the reward for low effort option was larger than the indifference point, which was set a priori. We also observed that participants were generally accepting more high/medium effort options in later trials, which suggested that indifference points were not static and shifted throughout the course of the task. To explore if indifference points varied

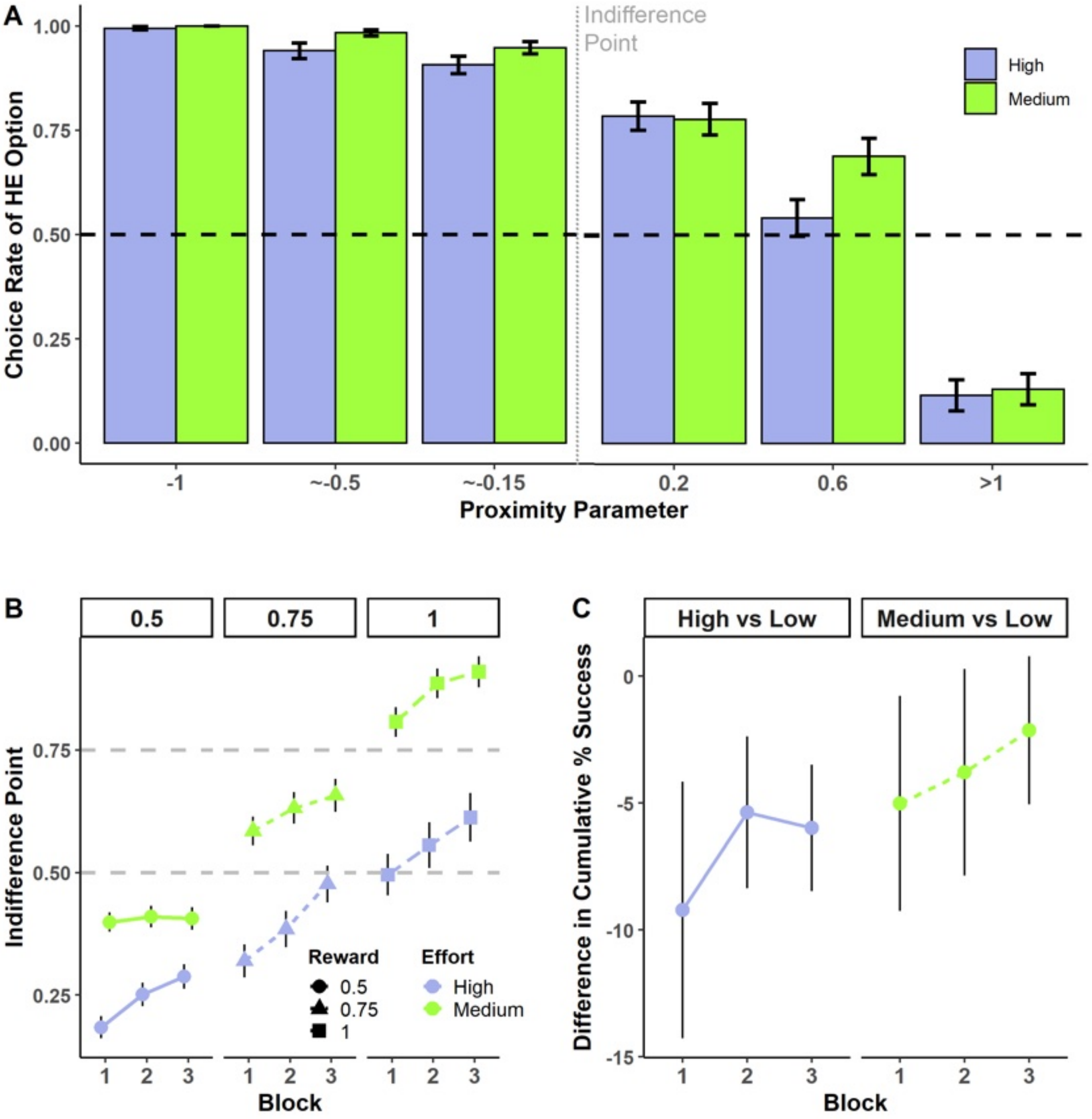


Figure 6.2: Caveats of designing an effort-based decision-making paradigm. **A)** Rate of selecting the higher effort (HE) option as function of proximity parameter. Participants prefer the more demanding option when the low effort option has no reward (proximity parameter = -1) and prefer the less demanding option when it offers the same reward as the more demanding option (proximity parameter $\geq$ 1). However, as the reward value approaches a proximity parameter of 0 (or the individual indifference point), selection of the higher effort options should approach .50. Instead, the data reveals that participants' preferences are generally biased towards the high effort option. **B)** Indifference points increase progressively throughout the task. **C)** Difference in cumulative success rates between high and low effort trials and medium and low effort trials throughout the task. Black bars signify the standard error of the mean.

across time, we modified the task by dynamically adjusting the indifference points throughout the task using a staircase procedure. In this sample (N=31), we saw that indifference points generally increased throughout the task, such that participants discounted higher effort rewards less with more time on task (see Figure 6.2B). As shown on Figure 6.2C, we also observed that the difference between the probability of success in low effort trials and higher effort trials was greater in earlier blocks than in later blocks. One plausible explanation, therefore, was that changes in indifference points were being driven by the reduction in differences in success rates, such that the more time on task, the better the calibration mechanism equalizes reward rates between effort levels, resulting in less discounting.

These preliminary findings from the behavioral pilot highlight several important considerations when developing effort-based decision-making paradigms. One consideration is that although performing effort online allows for experimental control of success rates, one needs to account for the shift in subjective values (i.e., indifference points) that occur as a consequence of these variations in reward rates. This is more manageable in passive effort paradigms, like the ones implemented in Studies 2 and 3 of the present work; however, in decision-making paradigms, shifting subjective values for effort-based preferences may generate choice patterns that are highly biased towards rewards with higher effort requirements, which can complicate the statistical modeling of choice data later on. Conversely, this also reveals an advantage for performing effort demands offline, after decision-making: although estimates of reward likelihood may differ between effort demand levels, at least subjective value estimates are not influenced by fluctuations in performance. To our knowledge, though, neuroimaging studies that have used paradigms with offline effort exertion have not accounted for the effect of success rate and/or reward probability in subjective value estimates (Aridan et al., 2019; Bernacer, Martinez-Valbuena, Martinez, Pujol, Luis, et al., 2019; Chong et al., 2017; Hogan et al., 2019; Massar et al., 2015; Suzuki et al., 2021, but see Arulpragasam et al., 2018), meriting consideration in future studies implementing these designs.

6.2 Limitations

Certain methodologies employed in this thesis unintentionally introduced limitations. Although the utilization of diverse methodologies facilitated the exploration of various facets of effort-based reward processing, it also restricted our ability to interpret the results in light of our previous findings. Notably, it would have been valuable to examine whether specific sub-regions of the mPFC were selectively involved in signaling different components of prospective net value and reward feedback. This investigation is particularly pertinent considering that the findings from Study 1 partially support the existence of a posterior-to-anterior gradient in value representation, as proposed elsewhere (Clithero and Rangel, 2014). While we had compelling reasons to employ EEG in addressing the research questions posed in Study 2, an exciting avenue for future research would be to pair paradigms that disentangle effort from probability costs with techniques with higher spatial resolution (e.g., EEG-fMRI) to explore how substrata of the mPFC signal specific features of net value.

An additional limitation is that several of our analyses may have suffered from lack of statistical power. Although we had sufficient power to test the main hypotheses of Study 1, we were unable to implement several of the desired supplementary analyses because too few studies met the constraints of these sub-analyses. Naturally, this limitation was outside of our control, since we were limited to available, published data from extant studies. Regardless, due to the number of studies included and the variety of paradigms used, we were forced to run supplementary analyses with a subgroup of studies that met a certain condition, instead of contrasting activation patterns in two conditions. Consequently, we could only make inferential conclusions about the robustness of the original findings instead of directly identifying differences in activation patterns between two conditions (e.g., physical vs cognitive effort, single offer vs difference in SV, etc.). Similarly, recent studies using EEG to study allocation of control for rewards have reported significant, but quantitatively small, effects for cue-related ERPs (Frömer et al., 2021; Grahek et al., 2022). These studies used similar passive effort paradigms to the ones utilized in Study 2 and report significant differences of 1 microvolt in late event-related potentials (i.e., P3b and CNV) with a sample of at least 40 participants (Frömer et al., 2021; Grahek et al., 2022). Had effect sizes from these studies been included in our a priori sample size estimation, we may have opted for a larger sample size in Study 2. However, another recent study which investigated cue-evoked FMT power during effort-based decision-making (Umemoto et al., 2022) also detected very modest effects with a relatively large sample size (N=77), thus it seems unlikely that increasing sample size would have truly allowed us to detect any effect in theta.

Another limitation of the present work is that we could not directly test any hypothesis of performance monitoring or behavioral adaptation. Due to the relatively small number of failed effort trials in Study 2, we were unable to look at the effects of negative performance outcomes. This would have been of crucial interest, since theta power has been repeatedly implicated in conflict and error monitoring, signaling of unexpected events, and translating prediction errors into behavioral shifts (Cavanagh et al., 2010; Luft et al., 2013; Mas-Herrero and Marco-Pallarés, 2014; van de Vijver et al., 2014). Furthermore, several theories suggest that ACC output, as marked by theta power, indexes need for control (Holroyd and Yeung, 2012; Shenhav et al., 2013). In Study 2, we explored relationships between theta power at cue and accuracy and reaction time in the effort tasks (not reported), however no effect was observed, presumably because accuracy was locked in our paradigm. Furthermore, because accuracy rates were deliberately high, we did not have enough unsuccessful trials after pre-processing to adequately analyze the effect of performance feedback on EEG signals. One potential solution would be to shorten the duration and demand of the effort manipulation so that we could have more effort trials. For example, recent studies that use a Stroop task as an effort manipulation adjust response time limits in order to render an 80% success rate (Frömer et al., 2021; Grahek et al., 2022), allowing for more effort trials with EEG data. Even within narrow ranges of success rates and reaction times, these studies were able to detect robust, albeit small, effects of EEG signals on accuracy and response times (Frömer et al., 2021; Grahek et al., 2022).

One additional limitation was our inability to isolate performance feedback from reward feedback in Study 2. This complicated the interpretation of findings, as both FMT and, albeit to a lesser extent, P3 has been shown to be sensitive to performance feedback (Glazer et al., 2018; Luft, 2014). To our knowledge the only study using effort-based reward with EEG experimentally isolated performance feedback from reward feedback by adding a probabilistic component to reward (Ma et al., 2014). While this strategy efficiently disentangled neurophysiological responses to each type of feedback, it also added another variable – reward uncertainty – that was outside the scope of the current work. Notwithstanding, results from Study 3 suggest that performance feedback maybe be more relevant than effort expenditure when learning stimulus-outcome associations. Therefore, developing paradigms where rewards remain contingent on performance but dissociate performance feedback from reward delivery will be particularly crucial for future research.

6.3 Future Directions

The findings presented throughout this thesis leave a number of open questions. One of the predominate hypotheses regarding the role of the ACC in effort-based decision-making is that it is involved in option comparison and action selection (Shenhav et al., 2013; Vassena, Holroyd, et al., 2017). Specifically, the ACC has been suggested to track choice difficulty as opposed to foraging value (Shenhav et al., 2014), the net value of rewards (Westbrook et al., 2019), or the subjective value of effort (Hogan et al., 2019). Furthermore, the pre-SMA, rostral ACC, and other frontoparietal areas have higher BOLD activity when choosing between high and low cognitive effort tasks voluntarily, as opposed to when the choice is predetermined (Schouppe et al., 2014), again suggesting a very important role for this network in comparison and selection of effortful options. Thus, one of the main goals of future research should be to identify to what degree the mPFC/ACC encodes for pure value representation and to what extent it is recruited for option comparison and action selection.

As described above, we designed and piloted an effort-based decision-making paradigm to accomplish these aims. Although we were forced to drop certain features (i.e., parametric measure of effort, proximity parameters, etc.), we were able to generate an effort-based decision-making paradigm that replicated discounting behavior while also controlling for unequal success rates between effort conditions (Figure 3). This paradigm is currently being adapted for EEG with the intent to identify to what extent FMT is recruited for single offer subjective value representation, option comparison, and action selection.

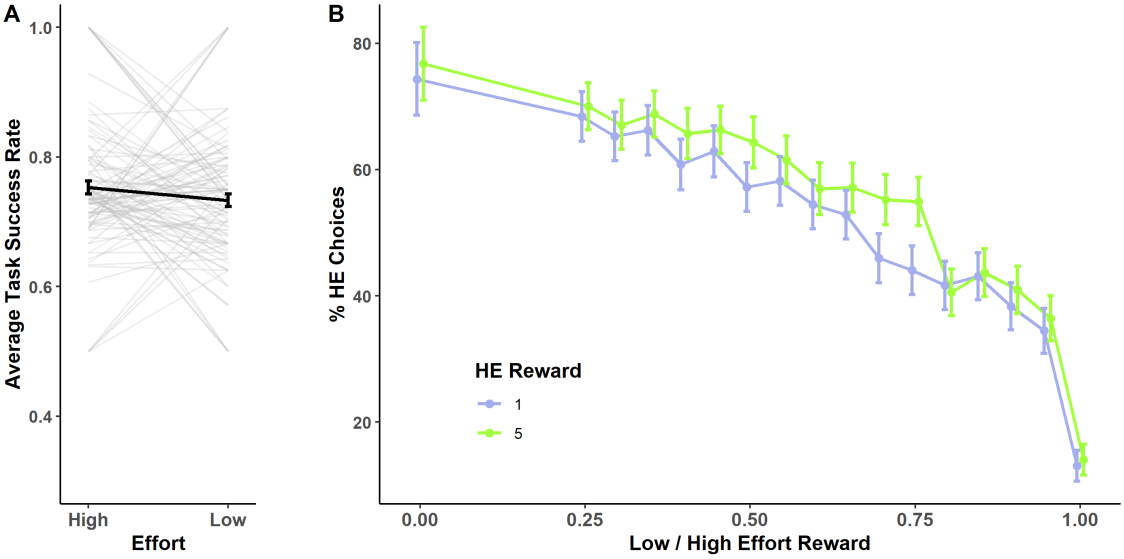


Figure 6.3: Behavioral results from simplified version of effort-based decision-making task. Data was collected from 105 participants. Participants that had no variance in their choices were removed, leaving a a final sample of N=96. **A)** Overall, there was no significant difference between success rates in the Low and High effort tasks (t(95)=1.28, p=0.20). However, there is a reasonable amount of individual variance in success rates overall which would need to be controlled statistically. **B)** The figure represents the percentage of high effort (HE) choices as a function of the ratio between the low effort reward offer and the high effort reward offer. In this version of the paradigm, there were two levels of fixed high effort reward (1 and 5 points). Bars represent the standard error of the mean.

Similarly, another open question from Study 3 is the degree to which effort modulates reward prediction errors. Although we did not identify any effects of effort on behavioral adaptation and learning rates, it is possible that cognitive effort had more subtle effects on cue prediction updating that were not captured in our indices of learning. For example, a recent study revealed that effort positively shifted RPEs, such that positive RPEs were enhanced and negative RPEs were attenuated by increasing physical effort demands (Jarvis et al., 2022). However, this effect in RPEs was coupled with a modest relationship between increased effort and higher cue selection accuracy (Jarvis et al., 2022). Specifically, improvements in cue selection accuracy were only detected in the high effort condition; in fact, cue selection accuracy was equivalent between medium effort and control condition and reduced for rewards that required low effort. Taken together, these findings suggest that effort may influence the mechanism by which reward outcomes are evaluated without resulting in large, detectable shifts in reward learning behavior. Thus, future research should focus on computational analyses that can parse apart the contributions of effort to reward prediction and pair these with neuroimaging techniques (e.g., EEG) to better elucidate the neural underpinnings of these processes.

Another highly relevant question is the extent to which probability of success influences perceptions of task difficulty and how this subsequently alters net value estimates of effort-based rewards. Self-report findings from Study 2 suggest an interactive effect between effort demands and reward probability: probability of success influenced participants' perceptions of task demand, and effort demands influenced their perceptions of likelihood of success, despite comparable success rates between conditions. This observation highlights the notable influence that perception of success has on the weight assigned to effort costs and suggests an interaction between these two factors. Both effort- and probability-discounting rely on similar brain circuitry (Bailey et al., 2016; Seaman et al., 2018) and are sensitive to DA-ergic manipulations, such that DA agonists enhance willingness to tolerate low reward probability (Floresco and Whelan, 2009; St. Onge and Floresco, 2009) and exert effort for reward (Salamone et al., 2012), while DA antagonists attenuate these tendencies. Furthermore, in humans, pharmacological enhancement of DA increases the willingness to exert effort for reward, specifically for low probability rewards (Soder et al., 2020; Wardle et al., 2011). This dopamine-dependent effect could be mediated by various factors, including as a reduction in the cognitive distortion of high and low probabilities (Ojala et al., 2018; Webber et al., 2020), diminished weight assigned to effort costs (Soder et al., 2020), or increased benefit of reward (Le Bouc et al., 2016; Skvortsova et al., 2017; Westbrook et al., 2020). Collectively, these findings suggest that effort and probability costs interact when evaluating effort-based rewards. Therefore, to better understand the contribution of effort costs and task difficulty to goal-directed behavior, future research must actively consider subjective estimates of probability of success in their paradigms.

Elucidating the unique and integrative effects of probability and effort on goal-directed behavior would also facilitate the identification of therapeutic targets for abnormal reward processing in different psychopathologies. Specifically, reduced willingness to exert effort for reward is a behavioral marker across a variety of psychopathologies, including major depressive disorder (Cooper et al., 2018; D. H. Treadway, 2011), schizophrenia (Cooper et al., 2019; Reddy et al., 2015), and Parkinson's disease (Chong et al., 2015; Le Heron et al., 2018). However, a growing body of work suggests that extent to which willingness to exert effort is altered in psychiatric and neurological conditions depends on the probability of reward, with some studies reporting reduced willingness to exert effort in clinical groups when rewards are less likely (Cooper et al., 2019; Reddy et al., 2015; M. T. Treadway, Bossaller, et al., 2012), while others report the opposite (Barch et al., 2014; hua Yang et al., 2014; M. T. Treadway et al., 2015). In Parkinson's disease, treatment with D3 and D2 agonists is associated with amelioration of motivational deficits (Chong et al., 2015; Le Heron et al., 2018; McGuigan et al., 2019) but the development of impulse control disorders, including increased risk-taking and excessive gambling (Voon et al., 2011; Voon et al., 2014), suggesting receptor- and circuitry-specific modulation of effort and probability costs. Furthermore, this altered sensitivity to reward probability information in effort-based rewards has been shown to be related to cognitive impairment in schizophrenia (Cooper et al., 2019) and associated with altered brain activity in patients with major depression (hua Yang et al., 2016). Willingness to exert effort for intermediate to high probability rewards, but not low probability rewards, was related to anhedonic symptoms in healthy subjects (M. T. Treadway et al., 2009), suggesting that altered integration of effort and probability costs may extend to subclinical populations as well. Thus, it is possible that cognitive and motivational impairments may contribute to maladaptive effort allocation in psychopathology and that the weighing of probability costs may be an important factor in those abnormalities. Hence, further research is needed to explore this aspect of effort-based decision-making.

Similarly, another important target for future clinical research is exploring how effort demands are evaluated throughout the distinct phases of reward processing, such as reward motivation, learning, and hedonic capacity. One of the main findings of the current work is that the impact of effort demand on reward value varies across stages of reward processing. This has implications for understanding effort-based behavior in both health and disease. Broadly speaking, in healthy humans, dopamine appears to differentially impact reward processing, such that pharmacologically enhancing DA (in a neurochemically non-specific manner) reliably increases willingness to exert effort and anticipatory responses to reward, but has an unclear impact on hedonic responses and learning (Webber et al., 2020). Conversely, in psychopathology, some aspects of effort and reward processing are impaired, while other functions remain largely preserved (Zald and Treadway, 2017). For example, in bipolar disorder, reward learning and hedonic responses appear relatively normal, while pursuit of goals and the willingness to work for rewards appear heightened even in remission (Alloy et al., 2015; Johnson et al., 2012). Therefore, an interesting proposal for future research would be to explore how effort is weighed throughout the stages of reward processing with the aim of identifying potential targets for treatment.

6.4 Conclusion

The aim of this thesis was to investigate the impact of effort demands on reward value. To achieve this, we conducted three studies that explored the effect of effort demands on different stages of reward processing. The first study categorically examined brain regions that were consistently involved in signaling effort demands and net value of prospective rewards. A meta-analysis of coordinate- and image-based fMRI data revealed that the pre-SMA is consistently activated for increasing prospective effort costs and deactivated for increasing net value, while the vmPFC shows the opposite pattern. This double dissociation suggests that the net values of effort-based rewards are integrated and signaled in the common valuation network and that the mPFC/ACC is also responsible for these functions.

To further explore the involvement of the mPFC/ACC in tracking the value of effort, we designed a second study that aimed to identify raw effort and net value signals across the stages of reward processing by fully dissociating reward probability from cognitive effort costs. Using scalp EEG recordings in two separate experiments, we observed that FMT power did not exhibit sensitivity to effort or net value during cue presentation. However, FMT power was found to be enhanced for rewards obtained through high levels of effort. These findings suggest that prospective effort demands have a limited impact on the evaluation of prospective rewards, but indicate an allocation of increased cognitive resources towards rewards earned through higher costs. Since rewards gained under higher effort were more salient at feedback, it followed that effort expenditure may modulate the learning of stimuli-outcome contingencies. In a third study, we found that learning rates are not affected by cognitive effort demands but, instead, that performance feedback influenced cue-value updating.

Together, these findings implicate that effort is generally weighed against prospective rewards at the cue phase, and that this occurs to a limited degrees in the striatum, but primarily in the vmPFC and mPFC/ACC. However, in the absence of option comparison and when reward probability is experimentally isolated from cognitive effort demand, the effect of effort was only detectable at feedback. Instead of reducing outcome-related EEG indices of attention and reward salience, effort expenditure enhanced these signals, suggesting that effort may actually augment as opposed to discount the salience of reward during feedback processing. This finding falls in line with proposed models that posit that the ACC is involved in effort prediction in service of adaptive effort allocation, although the current experiments were not adequately designed to directly test these hypotheses. Interestingly, the potentiating effect of effort at reward feedback did not translate to enhanced learning of stimuli-reward associations, suggesting that only performance feedback was used to guide behavioral adaptation. Future research will need to develop novel experimental paradigms to fully control for confounding variables that plague the current study of effort-based reward processing. With careful design, future studies will be able to fully elucidate how the weighing of effort demands differentially impacts reward value during the various stages of reward processing, potentially to better treat maladaptive effort allocation in psychopathology.

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ACC anterior cingulate cortex

DA dopamine

dlPFC dorsolateral prefrontal cortex

EEG electroencephalogram

fMRI functional magnetic resonance imaging

GLMM generalized linear mixed effects model

DS dorsal striatum

FMT frontal midline theta

LMM linear mixed effects model

MCC midcingulate cortex

mPFC medial prefrontal cortex

NAcc nucleus accumbens

OPC orbital prefrontal cortex

P3 component P300

pre-SMA pre-sensory motor area

rmANOVA repeated-measures ANOVA (analysis of variance)

SMA sensory motor area

SN substantia nigra

vmPFC ventromedial prefrontal cortex

VS	ventral striatum
VTA	ventral tegmental area