THE VALUE OF EFFORT: HOW DO WE MAKE DECISIONS WHEN EFFORT IS INVOLVED?

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STATEMENT OF ORIGINALITY

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ABSTRACT

Effort-based decision-making is an instance of value-based decision-making in which effort is the main cost associated with obtaining rewards. Despite the fact that we engage in this process on a daily basis, many assumptions regarding effort-based decision-making have not been tested yet. Furthermore, no comprehensive model of this type of decision-making has been proposed. Therefore, the main aim of this thesis was to introduce a novel Value-Effort Decision-Making (V-E-D-M) model of effort-based decision-making. The proposed model consisted of six processing stages: Representation, Valuation, Action Selection, Action Execution, Outcome Evaluation and Learning. Assumptions of this model were investigated in this thesis to verify their validity. More specifically, six areas relating to the V-E-D-M model were explored: the effects of manipulating 1) reward characteristics and 2) effort type on effort-based decision-making, 3) importance of effort/reward during different stages of effort-based decision-making, 4) importance of outcome feedback during effort-based decision-making, 5) effects of delaying Action Execution on effort-based decision-making, and 6) neural underpinnings of the effort-based decision-making process. These topics were explored in six experimental studies utilising a novel effort-based decision-making task developed for the purpose of this thesis. The results of these investigations showed that: 1) the effects of reward magnitude on effort-based decision-making depend on the stage of the process, as rewards seem to affect behaviour mainly during Action Selection, and less so during Action Execution; 2) changing reward valence affects effort-based decision-making, as people become more risk averse when losses are at stake, 3) reward reliability can potentially affect effort-based decision-making, but only when participants believe they can increase their chances of obtaining rewards through exerting effort, 4) reward values drive behaviour during Action Selection, whereas effort requirements determine behaviour during Action Execution, 5) increasing the informative value of outcome feedback does not affect effort-based decision making, and 6) delaying Action Execution affects effort exertion during this stage. The final V-E-D-M model incorporates these results.

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Dedicated to Tadeusz Nawrot (1925-2015)

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CHAPTER 1: General Introduction

Effort-based decision-making is an instance of value-based decision-making in which effort is the main cost associated with obtaining a reward. We face this type of decision-making whenever we deliberate if it is worth getting up from the couch to go to the gym, or when we decide whether we should put in the effort and resources to study for a university degree. Whenever we think about prospective effortful actions we need to analyse the options that are available to us by taking into account the costs and benefits associated with each option. From this we are then able to choose an action that is the most beneficial in the given circumstances (Rangel, Camerer, & Montague, 2008). There are several basic assumptions that appear to be commonly accepted in the literature focused on effort-based decision-making which will be covered in detail in this chapter.

Many researchers investigating effort-based decision-making processes tend to assume that:

1) Effort is aversive and given a choice we should normally prefer an option which requires less effort;

2) The aversive effects of effort can be overcome if high enough reward is at stake (in fact, some might go as far as to say that all effort we expend is driven by, and proportional to, rewards that are available);

3) Mental and physical effort tasks are likely to be underpinned by the same underlying decision-making processes and so behaviour during tasks that are mental or physical should be similar;

4) Decisions concerning effort are based on estimated costs and benefits, which might differ from the actual experienced costs and benefits of the outcome.

Investigations examining these four assumptions conducted so far, however, paint a much more complicated picture of the rules guiding effort-based decision-making than has generally been assumed (e.g. Brehm & Self, 1989; Camerer & Hogarth, 1999). Therefore, the general aim of this thesis is to investigate the assumptions regarding the decision-making process when effort is involved in order to verify their accuracy in different circumstances. The key goal is to examine the effects of manipulating the reward structure of a decision-making scenario on effort-based choice and effort execution. Potential differences between mental and physical effort processing, as well as the differences in behaviour during choice and execution are also investigated.

Broadly, the structure and content of the thesis is as follows: the first chapter of this work provides an overview of value-based decision-making models used to represent effort-based choice and effort exertion in animals and humans. It also discusses the prevailing claims about the driving forces behind effort-based decision-making. Why does this chapter take this focus? The key reason is that decision-making is a process of interest in many disciplines, including psychology, neuroscience, economics, political science and computer science. In essence, this thesis focuses on the development of our understanding of this process derived primarily from psychology and neuroscience, with some mention of studies from the economics domain, in the view that this work is likely to inform literatures beyond just psychology.

Chapter 2 describes the rationale behind the specific manipulations included in a series of six experiments examining effort-based decision-making forming the empirical part of this thesis. In Chapter 3 the methodology behind the experimental task design and data analysis is discussed. Chapters 4, 5, and 6 describe the results of experimental investigations along with their implications. Finally, in Chapter 7 the findings are discussed in the wider context of value-based decision-making. In addition, the limitations of the design used throughout are addressed and future directions for research on effort-based decision-making are suggested.

The remaining part of this chapter will be structured in the following way: first, a brief overview of effort-based decision-making and the brain networks involved in this process will be provided. This will be followed by a discussion of the existing models of decision-making and their components, which will end with a presentation of a new, updated model of effort-based decision-making: the Value-Effort Decision-Making (V-E-D-M) model. From this, there will be a review of studies dedicated to examining processing of effort during decision-making in the context of the V-E-D-M model. Here the discussion will highlight the issues that need to be addressed to increase the predictive value of the new model. The implications of these studies will be considered, and a rationale for the new set of experiments will be outlined.

1.1 Effort-based decision-making

In everyday life obtaining rewards can be seen as overcoming obstacles, which often requires expenditure of effort. Decision-making in such situations can be described as effort-based. On the most basic level, effort-based decision-making characterizes the processes employed when we face a choice between engaging in effortful actions to obtain rewards versus remaining idle and not obtaining rewards. It also describes situations in which we are required to choose between options associated with different amounts of reward and effort.

Most generally, in such scenarios effort can be described as the energetic cost associated with performing mental or physical actions (Navon & Gopher, 1979; Robert & Hockey, 1997). Physical effort has been defined as the energetic cost of physical movement (Navon & Gopher, 1979), whereas mental effort has been characterized as allocation of mental resources (Jansma, Ramsey, de Zwart, van Gelderen, & Duyn, 2007), or the demand for controlled information processing (Kool, McGuire, Rosen, & Botvinick, 2010). Some researchers suggest that mental and physical effort are processed in the same way by the same neural systems (e.g. Boksem & Tops, 2008; Botvinick & Rosen, 2009; Eisenberger, 1992), although contradicting evidence exists (e.g. Hosking, Cocker, & Winstanley, 2014; Schmidt, Lebreton, Clery-Melin, Daunizeau, & Pessiglione, 2012). Therefore, there appears to be some confusion about whether the underpinning mechanisms that support mentally effortful processes and physically effortful processes are fundamentally the same or not. This point will be revisited again later in the chapter.

Some studies suggest that in certain circumstances effort might be rewarding in and of itself (Kim & Labroo, 2011; Kivetz, 2003). That is to say, we may enjoy the act of putting in effort because we like to challenge ourselves, and that becomes a rewarding experience. However, generally, effort is considered to be aversive. The fact that we have to perform effortful actions tends to reduce our willingness to engage in an activity. This is often because the effort that the action entails generates negative affect towards it, and is therefore treated as a cost both in humans and in animals (Brosnan & De Waal, 2003; Garbarino & Edell, 1997; Kool et al., 2010; Kurniawan et al., 2010; Robert & Hockey, 1997). The Law of Least Effort (Hull, 1943) has been a useful formulation to understand the negative associations with having to perform a potentially effortful action. This law stipulates that given two actions leading to similar rewards, the one requiring less effort will be chosen. One of the implications of this formulation is that effort is an important factor that is taken into account when making decisions.

Indeed, a large set of studies suggests that effort influences decision-making by changing the value we attach to options (e.g. Bonnelle et al., 2014; Chong et al., 2015; Day, Jones, & Carelli, 2011; Day, Jones, Wightman, & Carelli, 2010; Hartmann, Hager, Tobler, & Kaiser, 2013; Minamimoto, Hori, & Richmond, 2012). More specifically, it has been proposed that there is an inverse relationship between the value of reward and the amount of effort needed to obtain it during decision-making. That is, the value of rewards is thought to decrease as effort associated with obtaining them increases – a phenomenon called *effort discounting* (e.g. Botvinick, Huffstetler, & McGuire, 2009; Hartmann et al., 2013). The extent to which the value of rewards is discounted depends on such characteristics of effort as duration and intensity (Bonner & Sprinkle, 2002). Interestingly, while there is speculation regarding effort discounting and its' application to both physical and mental effort, direct tests of the extent to which effort discounting pertains to both mental and physical effort has not be carried out.

Turning to evidence from pharmacological research, brain imaging, and clinical studies there is support for the view that effort is an important dimension that should be accounted for when studying decision-making. For example Croxson, Walton, O'Reilly, Behrens, and Rushworth (2009) investigated the neuronal correlates of effort-based cost/benefit calculations in humans using the functional magnetic resonance imaging (fMRI) technique. They observed activation in the ventral striatum (part of the basal ganglia) and anterior cingulate cortex (ACC) in response to reward- and effort-predicting stimuli; this activation depended on the amount of effort required to obtain the reward. Croxson et al. (2009) have taken these results to suggest that ACC and striatum regions might be important for processing of effort during decision-making. In line with this conclusion, other studies have found that ACC and the striatum activate in response to choices involving effort, even in the absence of extrinsic rewards (Boehler et al., 2011; Botvinick et al., 2009; Schouppe, Demanet, Boehler, Ridderinkhof, & Notebaert, 2014). In general, structures identified as important for effort processing during effort-based decision-making in humans include ACC, parts of the basal ganglia (particularly the striatum), as well as other parts of the brain such as the basolateral amygdala (BLA), supplementary motor area (SMA) and insula (e.g. Bijleveld et al., 2014; Botvinick et al., 2009; Burke, Brunger, Kahnt, Park, & Tobler, 2013; Croxson et al., 2009; Gepshtein et al., 2014; Kroemer et al., 2014; Kurniawan, Guitart-Masip, Dayan, & Dolan, 2013; Kurniawan et al., 2010; Meyniel, Sergent, Rigoux, Daunizeau, & Pessiglione, 2013; Prevost, Pessiglione, Metereau, Clery-Melin, & Dreher, 2010; Schmidt et al., 2009; Schmidt et al., 2008; Treadway et al., 2012). Overall, this suggests that there are neurological mechanisms that are activated when making a decision that involves choosing between options associated with different levels of effort exertion.

In addition to identifying parts of the brain responsible for effort processing, pharmacological, brain imaging, and clinical studies also point to an important role for the neurotransmitter dopamine during effort-based decision-making. To start with, there are several lines of evidence which suggest that the dopamine system supports the ability of organisms to compare the different options available to them, by guiding choice towards the most optimal outcome (e.g. Assadi, Yucel, & Pantelis, 2009; Gepshtein et al., 2014; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Kroemer et al., 2014; Schmidt et al., 2008). In conjunction, evidence for the important role of dopamine in effort processing in humans also comes from studies investigating effort-based choice and effort exertion in Parkinson's disease (PD) patients. PD is a neurodegenerative disorder affecting dopamine-producing cells in the substantia nigra pars compacta, part of the basal ganglia. It leads to reduced midbrain dopaminergic transmission. Studies suggest that one of the consequences of the reduction of dopamine levels in the brain of PD patients is a shift in cost/benefit analysis. This means that during effort-based decision-making, costs are weighted even higher than gains, which leads to a decreased willingness to exert effort (e.g. Baraduc, Thobois, Gan, Broussolle, & Desmurget, 2013; Chong et al., 2015; Gepshtein et al., 2014; Kojovic et al., 2014; Mazzoni, Hristova, & Krakauer, 2007). Nevertheless, the existing studies on effort-based decision-making in PD concentrate mainly on investigating physical effort exertion, and so provide little information about the effects of dopamine depletion on decisions regarding mentally effortful tasks. Existing studies do contribute, however, to the general claim that effort-based decisions recruit brain systems that involve the neurotransmitter dopamine.

To summarise, even though effort is generally thought to be aversive, people still often engage in effortful activities, on condition that the effort spent leads to attractive rewards. During the decision-making process the value of rewards is discounted by the amount of effort needed to obtain them. This process is thought to rely on several different brain structures, particularly ACC and the basal ganglia, and the neurotransmitter dopamine.

The next section of this chapter describes value-based decision-making models which can be used to characterize the precise mechanisms involved in effort-based decision-making. These models are useful because the way in which we process values while making decisions is an important factor that needs to be considered when assessing whether to perform an effortful action or not. The next section will end with a proposed version of the models which focuses specifically on processing of values when effort is required.

1.2 Value-based decision-making models in the context of effort-based decision-making

Value-based decision-making is a general term used to describe decision-making in situations in which we face a choice between options associated with different rewards and costs (e.g. effort). It is a process by which we compare different options and choose the one associated with '*the best possible outcome*' (largest reward/least cost). These '*best possible outcomes*' can be associated with primary rewards, such as food or ensuring safety (shelter), or secondary rewards, such as money. In this section six decision-making models (by: Rangel et al. (2008), Doya (2008), Kable and Glimcher (2009), Assadi et al. (2009) , Ernst and Paulus (2005), and Rigoux and Guigon (2012)) describing the components of value-based decision-making are characterized, their limitations are discussed, and a new, effort specific, value-based decision-making model is proposed based on the components of the previous models.

Within psychology and neuroeconomics, value-based decision-making is conceptualised in various different ways. Most commonly it is assumed to consist of several interdependent processing steps. However, the steps considered to be important for this process differ depending on the flavour of the model being proposed (see Table 1). Rangel et al. (2008) suggest that value-based decision-making is formed of five consecutive steps, relying on separate, although partly overlapping brain structures: 1) **Representation**, 2) **Valuation**, 3) **Action Selection**, 4) **Outcome Evaluation** and 5) **Learning**. Representation involves an analysis of the external state of the environment, the internal state of the decision-maker, and the attributes of the available courses of action (see also: Regan, 2014). During the Valuation stage attributes of available options (i.e. costs and benefits associated with them) are combined to form a subjective value of each option. During the Action Selection stage these subjective values are compared and the action which leads to an outcome of the highest value is selected. The Outcome Evaluation stage then follows, which involves assessing the desirability of an outcome. At this stage the discrepancy between the predicted and the experienced outcome is established. The difference between the two (i.e. expected and actual outcome) serves as a basis on which Learning occurs. As a consequence of Learning, decision-makers can update the action-outcome associations. This allows them, during the next similar decision-making scenario, to decide what to do based on a more accurate estimate of the outcome. The value-based decision-making model by Rangel et al. (2008) was motivated by the results of animal and human studies investigating the neurobiological basis of the decision-making process, as well as studies investigating different computational models of decision-making.

Table 1. Summary of stages included in different value-based decision-making models

Model	Stage					
	Representation	Valuation	Action Selection	Action Execution	Outcome Evaluation	Learning
Assadi et al. 2009		+	+	+		
Doya 2008	+	+	+		+	
Ernst et al. 2005		+	+	+	+	
Kable et al. 2009		+	+			
Rangel et al. 2008	+	+	+		+	+
Rigoux et al. 2012		+	+	+		

Similarly, Doya (2008) also based his model of value-based decision making on the results of neurobiological and computational studies. He suggested, however, that decision-making consists of four steps, rather than five: 1) **Representation**: recognizing the present situation, 2) **Evaluation**: evaluation of options in terms of rewards and punishments they would bring, 3) **Selection**: selecting an action in reference to one's needs, and 4) **Re-evaluation**: re-evaluating an action based on the outcome. These steps are broadly consistent with what Rangel et al. (2008) suggested. Although Doya (2008) does not include an explicit Learning stage, the re-evaluation stage could be broadly considered as a Learning type stage in which some form of updating occurs.

As with Doya (2008) and Rangel et al. (2008), Kable and Glimcher (2009) formulated their decision-making model based on neurophysiological studies in humans and non-human primates, but also on theoretical models in economics. They identified two critical steps in value-based decision-making: 1) **Valuation**, and 2) **Choice**. During the Valuation stage decision-makers integrate different dimensions (probability, effort, rewards, time) of each available option into a subjective value. This subjective value is thought to depend on the learned values of actions taken in the past, although Learning is not defined as a separate decision-making stage in this model. During the Choice stage the subjective values of different options are compared, and the option with the highest value is chosen. The action associated with this option is then passed on to the motor system. The two decision-making steps described in this model are roughly equivalent to the Valuation and Action Selection stages of Rangel et al. (2008) model and Evaluation and Selection stages of Doya (2008) model. It is worth pointing out that Kable and Glimcher (2009) do not explicitly distinguish steps such as Representation, Outcome Evaluation, or Learning. Even though these stages are implied in their model, it does suggest that their model is limited with respect to detailing in full all the potential stages required in a decision-making process.

In line with Kable and Glimcher (2009), Assadi et al. (2009), as well as Ernst and Paulus (2005) presented a simple stage model of decision-making. Assadi et al. (2009) suggested, based on the studies investigating the role of the neurotransmitter dopamine during decision-making, that value-based decision-making consists of two stages: 1) **Evaluation**, and 2) **Execution**. Evaluation is based on the analysis of costs and benefits associated with different options, and the outcome of this analysis leads to an overall preference towards one of the options. Execution, on the other hand, relies on motivation (i.e. mobilization of energetic resources) and planning a sequence of actions to achieve the goal. In this model Outcome Evaluation and Learning are not specifically mentioned, although the role of dopamine in these processes is discussed. This suggests that the authors consider them to be part of decision-making as well but without any explicit detailed description of them. Contrary to the conceptualization by Rangel et al. (2008) the Representation stage is not included in this model.

Furthermore, Ernst and Paulus (2005), in their attempt to create a framework integrating findings from decision-making research in psychology, neuropsychology, brain lesions studies, and functional neuroimaging studies, divided decision-making into three steps: 1) **Valuation:** forming preferences among options, based on costs and benefits associated with them, 2) **Selection and Execution**: selecting and executing an action based on the preferences formed during Valuation, and 3) **Evaluation**: evaluating the outcome. Again, Ernst and Paulus (2005) do not explicitly mention Learning as part of the decision-making process, although they do discuss it, suggesting that they consider it to be important. In addition, they also neglect to outline a representational stage in their decision-making model.

The most recent model of value-based decision-making to be proposed is by Rigoux and Guigon (2012). Their decision-making model, in which they focus on processes crucial for action execution, is primarily based on reinforcement learning approach, much like Rangel et al. (2008) model. Rigoux and Guigon (2012) model takes into account not only the processes underlying choice, but also the translation of choice into action and online monitoring of costs and benefits while actions are executed. They suggest that decision-making consists of the following three stages: 1) **Choice:** during which choices are made based on the estimates of costs and benefits associated with available options, 2) **Execution:** during which selected actions are translated into movements, and 3) **Updating**: during which behaviour is adjusted if change in the environment is detected. Therefore, this model includes steps equivalent to the Valuation and Action Selection stages in Rangel et al. (2008) model, but it does not include the Representation, Outcome Evaluation or Learning stages.

The reason why different value-based decision-making models described above do not include the same processes, even though they rely on a similar subset of neurobiological and computational studies, is not entirely clear. It seems that many of these models have been primarily created to define the scope of interest for literature reviews, which clearly varied (i.e. ranging from neurobiology of decision-making in animals and humans, neuroimaging, computational models etc.). Also, it is likely that the exact decision-making steps presented in each model depend on the brain structures and mechanisms that were of interest to the authors, which is potentially a problem because the models may not be comprehensive.

Nevertheless, despite their differences, all of the models described above seem in agreement that effort-based decision-making includes a Valuation stage (see Table 1), during which the costs and benefits of each option are assessed and combined into a subjective value. Most of the models described above also include an Action Selection stage, during which the option with the highest subjective value is chosen. Despite the fact that Outcome Evaluation and Learning are not explicitly included as separate stages in most of the models, each theorist still discusses these processes in the context of their models. Similarly, even though Representation forms part of only two out of the six models described above, it is implicitly assumed to take place before the Valuation stage in all of the models, as the descriptions of the models make reference to this. In light of this, the model that seems to be the most comprehensive is the value-based decision-making model by Rangel et al. (2008), as it explicitly mentions all of the stages described above. However, this model does not include one important stage present in the other models: the Action Execution stage, and this appears to be a major omission.

Assadi et al. (2009), Ernst and Paulus (2005) and Rigoux and Guigon (2012) all state that the processes involved in Action Execution are a crucial component of decision-making. First of all, initial considerations of effort and rewards, taking place during the Valuation stage, may be rather different from the considerations one engages in when one is about to execute an action. Just as one is about to execute an action one may revisit the value attached to the action as the potential costs become more salient. This might have consequences for the effort exerted during the task and the outcomes achieved.

Second of all, since what happens during the Action Execution stage determines the outcomes that are achieved, Action Execution has important consequences for Outcome Evaluation and Learning. This is especially true in situations in which effort is the most salient cost. In such cases the decision-maker needs to take into account during the Outcome Evaluation stage not only the rewards obtained, but also the amount of effort that was actually expended to obtain them. Only then the outcome of the decision-making scenario can be assessed in relation to the predictions from the Valuation stage and serve as a basis for learning. For these reasons, Action Execution seems to be an integral part of decision-making, at least in situations in which effort is the cost, which means that it should be included in any comprehensive model of effort-based decision-making.

Taking this into account, a new framework describing effort-based decision-making is proposed here under the name of Value-Effort Decision-Making (V-E-D-M) model. Within this new framework effort-based decision-making is conceptualized as a process consisting of six consecutive and interdependent steps: **Representation**, **Valuation**, **Action Selection**, **Action Execution**, **Outcome Evaluation** and **Learning** (see Figure 1). The following section describes the proposed steps of V-E-D-M model in more detail, listing the studies supporting the model assumptions and considering the issues that arise from the proposed model.

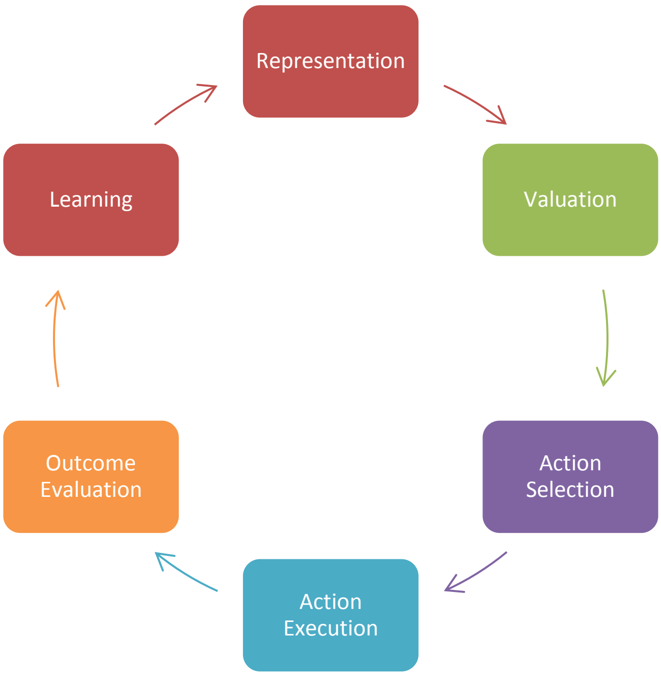


*Figure 1.*Value-Effort Decision-Making model

Representation and Valuation: In the proposed V-E-D-M model the **Representation** stage is involved in identifying: 1) the potential courses of action that are available in the decision-making scenario, 2) the internal state of the decision-maker, and 3) the external state of the environment. The Representation stage forms the basis on which valuation occurs at the **Valuation** stage. During the Valuation stage the costs (i.e. effort) and benefits (i.e. rewards) associated with each option identified during representation stage are estimated and integrated into a subjective value of an option. When assessing the benefits associated with different options factors such as the quality and quantity of a reward (Green & Myerson, 2004; Kacelnik & Bateson, 1997), as well as the valence (positive/negative) and salience (intensity, magnitude) of a reward (Ernst & Paulus, 2005) are taken into account. When assessing the cost of effort, factors such as intensity and duration are important (Burke et al., 2013; Choi, Vaswani, & Shadmehr, 2014; Gepshtein et al., 2014; E. D. Klein, Bhatt, & Zentall, 2005; Le Bouc & Pessiglione, 2013). The V-E-D-M model also assumes that during the valuation stage the values assigned to rewards associated with different options are discounted by effort costs to form subjective values. The subjective value of each option is abstract (it is a subjective construct that indicates the general positive or negative property overall of each option) – it is a form of common currency which drives choice during the Action Selection stage (Brosch & Sander, 2013). The subjective value of an option is also thought to be context dependent, i.e. the value assignment depends on the external environment (e.g. reliability of reward predicting cues), as well as internal factors (e.g. motivation or learning history of similar past situations the decision-maker has faced) (Doya, 2008).

Evidence in support: In line with the proposed **Representation** stage of the V-E-D-M model, animal neuronal recording studies and human fMRI studies show that the presence of stimuli predicting different levels of effort and reward produces anticipatory signals in the brain. These signals reflect the amount of effort to be exerted and the amount of reward associated with these stimuli (Hosokawa, Kennerley, Sloan, & Wallis, 2013; Kroemer et al., 2014; Kurniawan et al., 2013; Pasquereau & Turner, 2013).

Furthermore, the V-E-D-M model assumes that during the Valuation stage the values assigned to rewards associated with different options are discounted by effort costs. Results of human and animal studies support this assumption, as humans and animals have indeed been found to weigh the value of potential rewards against the amount of effort that is required to obtain them (*effort discounting*) (e.g. Day et al., 2011; Day et al., 2010; Kurniawan et al., 2010; Prevost et al., 2010). In general, it has been observed that as effort increases, the desirability of the reward decreases (Bonnelle et al., 2014).

Another assumption regarding the Valuation stage of the V-E-D-M model states that the subjective value generated during this stage is context dependent, which means that it depends on the internal state of the decision-maker, as well as the external state of the environment. This assumption is supported by the results of studies which found that the effect of rewards on behaviour is mediated by external factors (e.g. task complexity, reward reliability, feedback, time pressure, personal wealth), as well as internal factors (e.g. motivation, personality, ability) (Bonner & Sprinkle, 2002; Camerer & Hogarth, 1999; Doya, 2008; Ernst & Paulus, 2005; Westbrook, Kester, & Braver, 2013).

As far as the external factors are concerned, task environment is thought to have a profound influence on effort-based decision-making (N. M. Klein & Yadav, 1989; Le Bouc & Pessiglione, 2013; Samuels & Whitecotton, 2011). For example, task complexity has been shown to affect the attractiveness of available rewards, with the reward seen as the most attractive when the task is hard, but less attractive when the task is easy or impossible (Brehm & Self, 1989). Environmental factors, such as the presence of an observer, have also been found to influence effort exertion during a task. Findings show that this can lead to increases in cardiovascular markers of effort, as well as greater effort expenditure (Gendolla & Richter, 2006; R. A. Wright, Dill, Geen, & Anderson, 1998).

Internal factors have also been found to play an important part in the Valuation processes, in line with the assumption of the V-E-D-M model. For instance, personality traits, such as 'need for cognition' (i.e. tendency to engage in and enjoy effortful cognitive endeavours) have been found to influence preferences regarding cognitive effort (Cacioppo, Petty, Feinstein, & Jarvis, 1996; Westbrook et al., 2013). Participants with higher 'need for condition' show greater willingness to exert mental effort. Also, skill has been shown to determine the extent to which available rewards influence effort exertion: when people lack the skills necessary to complete the task, no amount of additional effort can improve performance and increase chances of success (Awasthi & Pratt, 1990; Bonner, Hastie, Sprinkle, & Young, 2000). Furthermore, emotional arousal has been found to increase effort exertion and decrease subjective experience of effort, regardless of monetary rewards (Schmidt et al., 2009). Finally, mood has also been found to influence the appraisal of effort, with task difficulty perceived to be higher in negative mood states (e.g. Gendolla & Brinkmann, 2005; Richter & Gendolla, 2006).

Outstanding issues: The V-E-D-M model assumes that during the valuation stage reward values are discounted by the amount of effort that is required to obtain them, and that the internal state of the decision-maker, as well as the external state of the environment can have an impact on this process, for which there is empirical support. However, the model also assumes that factors such as reward magnitude, valence, and reliability can have an impact on the Valuation stage. Nevertheless, what this impact might be is less certain, as it has not been directly examined so far. The question, therefore, is: what effect does changing reward magnitude, valence or reliability have on effort-based decision making? This question has yet to be explored in any systematic way in the literature on effort-based decision-making thus far.

Moreover, the model assumes that certain characteristics of effort (e.g. duration or intensity) have an impact on valuation, but it does not discuss the effects different types of effort (i.e. mental or physical) have during the Valuation stage. This is an empirical question that still needs to be addressed. Therefore, to increase the validity of the model two issues need to be addressed: 1) the impact of changing the reward magnitude, valence, and reliability on effort-based decision-making, and 2) the potential differences in the effects of conceptually similar but in practice very different costs such as mental and physical effort. This thesis aims to address these issues.

Action Selection and Action Execution: According to the V-E-D-M model, **Action Selection** relies on subjective values of options computed during the Valuation stage. During Action Selection these subjective values are compared and the option with the highest value is chosen (Koopmans, 1960; Neumann & Morgenstern, 1944; Prelec & Loewenstein, 1991; Rachlin, Battalio, Kagel, & Green, 1981). During **Action Execution** the preferences of the decision-maker expressed through choice are translated into actual actions. In the models that have included this stage (Assadi et al., 2009; Ernst & Paulus, 2005; Rigoux & Guigon, 2012), effort during execution is thought to be driven by reward values (Bijleveld, Custers, & Aarts, 2009, 2010, 2011; Bijleveld et al., 2014). However, there is some evidence to suggest that the execution of an action is not driven by rewards *per se.* The challenges come from studies investigating the Theory of Motivation by Brehm and Self (1989). According to Brehm and Self (1989) behaviour is driven by the resource conservation principle. Their Theory of Motivation (1989) assumes that effort associated with an action is of primary concern to the decision-maker, and that rewards are only used as a benchmark to assess if a particular amount of effort is worth incurring.

Evidence in support: Many decision-making models (e.g. Assadi et al., 2009; Ernst & Paulus, 2005; Rigoux & Guigon, 2012) assume that reward values drive Action Selection and Action Execution. However, others (e.g. Brehm & Self, 1989) claim that what actually influences behaviour (at least during Action Execution) are the effort requirements of a task, and that rewards serve only as a benchmark determining the maximum level of effort decision-maker is willing to exert. Evidence from studies examining effort-based decision-making supports both of these claims.

Several studies suggest that effort requirements drive effort exertion. For example, people have been found to modulate their effort exertion in accordance with task demands, in the presence as well as absence of reward (Brehm & Self, 1989; Eubanks, Wright, & Williams, 2002; Gendolla, Wright, & Richter, 2012; R. A. Wright, 2008). Various studies have also shown that people invest the most effort on tasks of medium difficulty, and less effort when the tasks are very easy or very difficult to complete, and that this effect is independent of the rewards associated with these tasks (e.g. Gendolla et al., 2012; Richter, Friedrich, &

Gendolla, 2008; Richter & Gendolla, 2006; Smith, Baldwin, & Christensen, 1990; e.g.R. A. Wright, 1984; R. A. Wright, 1996; R. A. Wright & Kirby, 2001).

At the same time, another literature shows that rewards have an energizing effect on goal-directed behaviour. In a variety of tasks involving both mental and physical effort, humans and animals have been found to increase their effort expenditure when the rewards at stake are high (Bijleveld et al., 2009, 2010, 2011; Bijleveld, Custers, & Aarts, 2012; Endepols et al., 2010; Krebs et al., 2012; Meyniel et al., 2013; Pessiglione et al., 2007; Schmidt et al., 2009; Schmidt et al., 2012; Treadway, Buckholtz, Schwartzman, Lambert, & Zald, 2009; Veling & Aarts, 2011; Watanabe, 2007).

Outstanding issues: The implicit assumption of many decision-making models is that both Action Selection and Action Execution are driven by rewards (albeit discounted by costs in the case of Action Selection). However, this assumption has never been tested directly, even though there is evidence to suggest that performance (during Action Execution at least) might be determined by task demands. Therefore, the main question regarding the Action Selection and Action Execution stages is: what drives behaviour during these stages? Is it the subjective value of reward, or is it the amount of effort that needs to be put in? To answer this question, a direct comparison of the effects of effort requirements and rewards on behaviour during Action Selection and Execution would need to be conducted. One of the aims of this thesis is to perform such a comparison.

Outcome Evaluation and Learning: According to the V-E-D-M model, during the **Outcome Evaluation** stage desirability of the experienced outcome is assessed and compared to the predictions made during the Valuation stage. The discrepancy between the predicted and experienced outcome is thought to serve as a basis for updating the action-outcome associations in the brain, triggering **Learning** (Rangel et al., 2008). Reward feedback and effort exerted during a task are thought to be the main factors taken into account during the Outcome Evaluation and Learning stages of the V-E-D-M model.

Evidence in support: In line with the assumptions of the V-E-D-M model, effort exerted during a task has been found to influence the Outcome Evaluation stage, by increasing sensitivity to rewards. For example, both humans and animals were found to show a greater preference for rewards that follow greater effort (Alessandri, Darcheville, Delevoye-Turrell, & Zentall, 2008; Clement, Feltus, Kaiser, & Zentall, 2000; Johnson & Gallagher, 2011; Kacelnik & Marsh, 2002; E. D. Klein et al., 2005; Lewis, 1964). It has also been shown that people are more sensitive to rewards when the task requires high effort expenditure (Bijleveld et al., 2012; Hernandez Lallement et al., 2014). This suggests that even though effort might decrease the subjective value of rewards during the Valuation stage, it can also increase sensitivity to these rewards in the Outcome Evaluation stage.

As far as the Learning stage is concerned, there seems to be plenty of evidence showing that learning is driven by a discrepancy between the actual and predicted reward. Midbrain dopaminergic transmission is thought to be crucial for this process. It has been shown that dopaminergic neurons in the brain react strongly to unpredicted outcomes, encoding reward prediction errors. This dopaminergic signal becomes less and less pronounced with experience of certain outcomes within a particular context, which is thought to reflect learning (Schultz, 1998, 2000, 2002, 2007; Schultz, Apicella, & Ljungberg, 1993; Schultz, Dayan, & Montague, 1997; Schultz & Dickinson, 2000). There is, however, no evidence that similar prediction errors signals regarding effort are encoded in the brain. In fact, one study shows that humans are actually poor at predicting the amount of effort that a task is going to involve. Fennema and Kleinmuntz (1995) asked participants to estimate effort and accuracy associated with performing tasks which differed in terms of information display organization and number of alternatives. Their estimations were found to be considerably off the mark, even after they have had a chance to interact with the task and experience feedback. Another study showed that effort feedback had no effect on performance (Creyer, Bettman, & Payne, 1990), suggesting that learning about effort is different from learning about rewards.

Outstanding issues: Even though reward feedback is thought to be an important factor during the Outcome Evaluation and Learning stage, the exact effects of different types of reward feedback on effort-based decision-making have not been examined. Therefore, any proposals regarding the effects of reward feedback on various stages of effort-based decision-making are currently speculative.

Furthermore, the V-E-D-M model assumes that learning from previous outcomes is the main factor influencing representations in situations in which we face similar decision-making scenarios repeatedly (particularly when sequential learning from repeated decisions is required). Since representations guiding choice are updated each time we experience an outcome of a decision-process, there should be differences between situations in which we repeatedly make choices and experience outcomes after each choice, from situations during which the experiences of outcomes are postponed until all choices are made first.

Nevertheless, how decision-making in these two situations might be different has never been investigated directly. Therefore, it remains an empirical question if the distinctions made in the model bear out in the evidence. Consequently two issues regarding Outcome Evaluation and Learning require experimental support: 1) the effects of different types of outcome feedback on effort-based decision-making, as well as 2) the differences in decision-making when learning can and cannot take place. These issues will be examined in this thesis.

Summary of the models of value-based decision-making

There are various models describing how decisions are made which are applicable to situations in which we face a choice between options that involve different levels of effort and reward. They conceptualize decision-making as a process consisting of several steps, although they differ in terms of what steps they include. The model that seems to be the most comprehensive, by Rangel et al. (2008), divides the decision-making process into five steps: Representation, Valuation, Action Selection, Outcome Evaluation and Learning. However, this model does not include one important step which plays a crucial role in other models (Assadi et al., 2009; Ernst & Paulus, 2005; Rigoux & Guigon, 2012) – the Action Execution stage. For this reason, in this thesis a novel model including all of the relevant stages mentioned above, the V-E-D-M model, is proposed. The V-E-D-M model concentrates specifically on effort-based decision-making, and assumes that this process consists of six consecutive steps: Representation, Valuation, Action Selection, Action Execution, Outcome Evaluation and Learning. Furthermore, it makes certain assumptions about what happens during these stages. However, some of these assumptions have not been explicitly tested so far. For example, the model assumes that during the Valuation stage costs and benefits associated with different options are combined into subjective values. Nevertheless, the exact effects of manipulating reward valence/magnitude/reliability or important cost characteristics (such as whether effort is mental or physical) on the cost/benefit analysis during this stage have not been investigated yet. Furthermore, the model assumes that feedback-driven learning is an important part of the decision-making process, however, the exact importance of reward feedback or the effects of learning on decision-making have not been investigated so far. The aim of this thesis is to test the assumptions listed above to improve on the predictive value of the new value-effort decision-making model and to increase our understanding of the effort-based decision-making process.

1.3 Summary of work on value-based decision-making and effort-based decision-making

Effort-based decision-making describes a process by which animals and humans choose between options associated with different levels of effort and reward. It is a process mediated by brain structures such as the ACC and the basal ganglia, and the neurotransmitter dopamine. Although many models that can be used to describe effort-based decision-making exist, all of them seem to be missing some important components of this process. Therefore, in this chapter a novel framework for investigating effort-based decision-making, the V-E-D-M model, was proposed. The evidence from effort-based decision-making studies seems to provide initial support for this new model. Human and animal studies conducted so far suggest that people form representations of options available to them during effort-based decision-making tasks. They also show that people engage in the calculations of subjective values of options and that these calculations drive the choices people make. In addition, some studies suggest that rewards serve as a benchmark for effort investment, whereas other studies suggest that effort exerted is driven by, and proportional to, available rewards. They also confirm an important role for Outcome Evaluation and Learning during decision-making.

Despite the strong support for the V-E-D-M model, some assumptions made by the model have never actually been tested. To add credence to the assumptions, the following empirical questions are raised:

1) What are the effects of manipulating reward magnitude/valence/reliability on effort-based decision-making?
2) Does the impact of mental and physical effort on decision-making differ?
3) Which factor, reward value or effort requirement, drives Action Selection and Action Execution?
4) What is the effect of reward feedback on effort-based decision-making?
5) To what extent does learning influence effort-based decision-making?

The main aim of this thesis is to address each of these questions and to test the assumptions of the proposed model. Furthermore, an additional question that this thesis will also attempt to answer relates to the role of neurotransmitter dopamine during effort-based decision-making. The key reason for this is that the scope of the studies investigating the role of this neurotransmitter during effort-based decision-making is usually limited to investigating physical effort and not mental effort. Also, the role of dopamine in effort based-decision-making is still unclear and so additional empirical work would illuminate key issues that would inform research on effort-based decision-making. Chapter 2 provides a further rationale for investigating these questions, and lists specific hypotheses derived from these questions to be explored in this thesis.

CHAPTER 2: Aims and Hypotheses

V-E-D-M model provides a useful framework for investigating effort-based decision-making, as evidenced by the results of previous studies described in Chapter 1. However, the model also makes certain assumptions which still need to be examined.

1) **Reward manipulations:** The V-E-D-M model assumes that manipulating reward magnitude, reward valence, and reward reliability should have an impact on the Valuation stage, and therefore potentially on the whole decision-making process. However, the impact of changing these reward characteristics has not been directly investigated in the context of effort-based decision-making.
2) **Effort manipulations:** The V-E-D-M model assumes that manipulating important effort characteristics, such as effort type (i.e. whether it is mental or physical) should have an influence on the Valuation stage. However, there have been few direct comparisons of mental against physical effort when examining effort-based decision-making.
3) **Importance of effort/reward during Action Selection and Action Execution:** The V-E-D-M model assumes that Action Selection and Action Execution are driven by the subjective values assigned to options during the Valuation stage. These subjective values depend on the reward values and effort requirements associated with different options. However, which one of these factors plays a more important role during Action Selection and Action Execution is less clear.
4) **Outcome feedback:** The V-E-D-M model assumes that feedback following Action Execution plays an important role during effort-based decision-making because it serves as a basis for updating the representations on which the Valuation stage is based. Nevertheless, how different types of feedback affect this process has thus far remained unexplored.
5) **Delayed Action Execution:** According to the V-E-D-M model the discrepancy between expected outcome and actual outcome (i.e. prediction error) forms the basis of learning and updating representations of the decision problem. This influences future decisions made in similar situations. This means that if decisions are taken in the absence of regular outcome feedback, (e.g. all effort-based decisions are made in advance of receiving outcome feedback), then this should lead to differences in

updating relative to situations in which outcome feedback is received directly after each effort-based choice is made. However, this assumption has not been tested yet.

6) **Neural underpinnings:** The V-E-D-M model has been informed by models based on neuropsychological and neurobiological studies investigating effort-based decision-making. Thus, it follows that the brain structures (e.g. basal ganglia) and neurotransmitters (e.g. dopamine) identified as important for processing of effort during different stages of decision-making in these models also play a role in effort processing during the stages of V-E-D-M. However, this assumption needs to be verified, especially as far as the role of dopamine is concerned, since most of the studies on this neurotransmitter in humans have only looked at the role of dopamine during physical effort exertion, and not extended this work to mental effort exertion.

In the remainder of this chapter various studies relevant to the areas described above will be reviewed, and based on these studies testable hypotheses will be formulated to be investigated in the empirical chapters of this thesis.

The following chapter is structured as follows: first studies examining the effects of manipulating reward magnitude, valence, and reliability, as well as the effort type (mental or physical) on effort-based decision-making are discussed. Second, studies investigating the factors driving behaviour during Action Selection and Action Execution are described. This is followed by an evaluation of studies scrutinizing the effects of feedback and learning on effort based decision-making. Finally, the role of dopamine during different stages of decision-making, as defined by V-E-D-M, is discussed.

2.1. Reward manipulations

2.1.1 Magnitude

According to the V-E-D-M model, manipulating reward magnitude should have an effect on the Valuation stage of effort based decision-making. More specifically, increasing reward values should lead to increased subjective values of different options, leading to increased willingness to choose and execute effort. Evidence gathered so far seems to provide strong support for this assumption. Studies investigating effort-based decision-making have generally found that higher rewards increase participants' willingness to choose effortful options and exert effort (Bijleveld et al., 2012; Bijleveld et al., 2014; Bonnelle et al., 2014; Burke et al., 2013; Capa, Bustin, Cleeremans, & Hansenne, 2011; Chong et al., 2015; Croxson et al., 2009; Hartmann et al., 2013; Kool & Botvinick, 2014; Krebs et al., 2012;

Kurniawan et al., 2013; Le Bouc & Pessiglione, 2013; Marien, Aarts, & Custers, 2014; Pas, Custers, Bijleveld, & Vink, 2014; Pessiglione et al., 2007; Treadway et al., 2009; Zedelius, Veling, & Aarts, 2011). The effect of rewards on effort processing is thought to be pronounced, to the point that reward cues are thought to increase effort expenditure even when they are presented below the threshold of awareness (subliminally) (Aarts, Custers, & Veltkamp, 2008; Bijleveld et al., 2009, 2010, 2011; Custers & Aarts, 2010; Pas et al., 2014; Pessiglione et al., 2007; Zedelius et al., 2011).

A straightforward interpretation of the findings presented above would be that increasing the amount of rewards available in a decision-making scenario leads to an increased willingness to exert effort at the time of Action Selection and Action Execution. However, the problem with this interpretation is that all of the studies investigating the effect of reward magnitude on effort-based decision-making looked at the relative, rather than absolute values of rewards. In such a set-up it is impossible to disentangle the effect of absolute reward magnitude from the effect of relative reward magnitude – as participants can base their decision either on the absolute monetary value ('I choose option A over option B because it is associated with a monetary reward of 15p, rather than 5p') or the relative monetary value ('I choose option A over option B, because it is associated with a reward that is three times higher'). This is an important distinction, as in certain circumstances different behaviour during Action Selection and Action Execution would be expected depending on which aspect of the reward participants concentrate on. If absolute reward values matter, increasing the monetary values of rewards within a task should lead to an increased willingness to execute effort on this task. If, however, it is the relative value of reward that matters, proportional increase of all the reward values available in the task (e.g. multiplying the reward values by two) would have no effect on participants' willingness to exert effort in this task. Therefore, the influence of reward magnitude on the final value generated during the valuation stage still needs to be investigated.

In the standard effort-based decision-making studies conducted to date the potential impact of relative and absolute reward values on Action Selection and Action Execution cannot be determined, because these studies utilise a within-subject design. At the same time comparisons between separate studies employing different reward magnitudes are also not possible due to methodological differences between the studies. Ideally, what is needed is an experimental set-up in which effort-related behaviour of one group that performs an effort-based task for smaller rewards (Small Reward group) is compared with a group that performs the exact same task for larger rewards (Large Reward group). If the absolute reward magnitude matters in such circumstances, then we would expect participants in the Large Reward group to be more willing to choose effortful options and put in effort, as compared to participants in the Small Reward group. If, however, processing during the Valuation stage relies on the relative values of rewards, then we should not see any differences between the Small Reward group and Large Reward group, providing that the difference between rewards is proportional between the tasks.

Therefore, in this thesis choice and execution of effortful actions (mental and physical) will be examined in two groups of participants: one experiencing large rewards, and one experiencing small rewards. In accordance with the basic interpretation of the results of the studies conducted so far, it is hypothesised that participants in the Large Rewards group will show greater willingness to choose and execute effortful actions than participants in the Small Rewards group.

2.1.2 Valence

According to the V-E-D-M model, reward magnitude is not the only reward characteristic with the potential to influence effort-based decision-making. Valence of reward, i.e. whether it is positive or negative, should also affect the Valuation stage and other stages that follow. Therefore, according to the V-E-D-M model we should expect decision-making in situations where we need to put in effort to gain monetary rewards to be different from situations in which we need to exert effort to avoid losing monetary rewards. Unfortunately, the evidence from studies examining the effects of gains and losses on effort-based decision-making is scarce, and so this assumption requires further investigations. However, there is substantial work examining the impact of gains and losses on decision-making in general, to which this review can look to in order to generate predictions.

Typically, people are thought to be more sensitive to losses than they are to gains, and therefore more risk-averse in the face of losses as compared to gains, at least when they make risk-based decisions (Kahneman & Tversky, 1979; Tom, Fox, Trepel, & Poldrack, 2007). This suggests that gains and losses might be processed differently. Further evidence for this claim comes from studies investigating brain activations in response to gains and losses (Elliott, Friston, & Dolan, 2000; Ino, Nakai, Azuma, Kimura, & Fukuyama, 2010; Litt, Eliasmith, & Thagard, 2008; Yacubian et al., 2006). For example, Ino et al. (2010) in their fMRI study found that gains compared to losses produced greater activation in the right putamen and nucleus accumbens. Yacubian et al. (2006), using the same brain imaging technique, observed reward-associated signals during outcome anticipation and evaluation in the ventral striatum, whereas losses were found to be represented in the amygdala. Furthermore, Hernandez Lallement et al. (2014) observed activation in the anterior insula that was specific to losses incurred after exerting mental effort, whereas the ACC and nucleus accumbens were activated during effort exertion for monetary rewards. The insula has also been found to be important for encoding worse-than-expected outcomes in an experiment where participants had to exert physical effort to obtain monetary rewards or avoid losing money (Kurniawan et al., 2013).

Nevertheless, other studies suggest that situations in which we want to obtain a reward and the situations in which we want to avoid losses are processed in the same way and rely on the same brain networks (e.g. Boksem & Tops, 2008). For example, the mesocorticolimbic dopamine system, and ventral striatum in particular, are thought to be responsible for encoding relative values of expected outcomes, regardless of whether they are appetitive or aversive (Brooks & Berns, 2013; Brooks et al., 2010). Tom et al. (2007) in their fMRI study showed increased brain activity for gains and decreased activity for losses in a set of brain structures including the dorsal and ventral striatum and the ventromedial prefrontal cortex (vmPFC) during risk-based decision-making, suggesting that gains and losses might in fact be processed within the same brain structures.

Regardless of the plethora of findings regarding processing of gains and losses from brain imaging studies described above, the investigations of behavioural differences between gaining and losing money are scarce, especially in the context of effort-based decision-making. Therefore, not enough evidence exists to support the assumption of the V-E-D-M model which states that reward valence impacts the valuation stage of decision-making. Consequently, one of the aims of this thesis is to examine the impact of gains and losses on effort-based behaviour. In line with the assumption of the model, it is hypothesised that there will be differences between effort processing in response to gains and losses, however the direction of the effect is hard to determine. If indeed losses are more psychologically salient than gains, people experiencing losses should select options associated with less effort because they are associated with a lower risk of failure. At the same time, during Action Execution people should exert more effort and attempt to be more accurate in order to minimize the risk of losses.

2.1.3 Reliability

According to the V-E-D-M model, in addition to reward magnitude and valence, the reliability with which reward-associated cues predict the rewarding outcome is thought to be an important factor influencing the Valuation stage. However, the effects of reward reliability have not yet been investigated in the context of effort-based decision-making.

Nevertheless, some studies of this process have employed a reward structure in which acquisition of rewards after effort expenditure was not guaranteed (i.e. there was a probabilistic relationship between performance and reward). Even though the main aim of these studies was not to investigate the effects of reward reliability on effort-based decision-making, they can still provide some useful insights into the impact that this factor is likely to have on effort-based decision-making.

For example, in their physical effort task, Kurniawan et al. (2013) awarded one group of participants with rewards on 80% of successful trials, and compared their performance with that of a group which received rewards 20% of the time. They found that participants were faster to respond and faster to reach the target force level when the probability of obtaining a reward was high. Treadway et al. (2009) also presented participants with trials during which acquisition of reward after effort exertion was not guaranteed. There were three possible probability levels of obtaining reward: 88%, 50%, and 12%. Participants were found to select more high effort trials when the probability of obtaining rewards was the highest. However, in this experiment participants were informed in advance of the probability of obtaining a reward, so the study was investigating decision-making under risk, rather than uncertainty.

Studies described above provide some, although very limited, insight into the effects of manipulating reward reliability on effort-based decision making. They suggest that increasing the probability of obtaining rewards increases the willingness to select and execute effortful actions. However, in the absence of a larger number of studies manipulating reward reliability when effort is required, it is impossible to assess the validity of the assumption made by the V-E-D-M regarding the effects of reward reliability on effort-based decision-making. One of the aims of this thesis is to address this issue. In accordance with the assumptions of the V-E-D-M model and previous findings it is predicted that there will be a positive relationship between the probability of obtaining rewards and the willingness to choose and execute effort. More specifically, it is expected that greater probability of attaining a reward will be associated with greater willingness to choose high effort options that are associated with this reward.

2.2 Effort manipulations

According to the V-E-D-M model, not only reward manipulations but also changes in effort requirements should have an impact on the Valuation stage. While there is substantial evidence to suggest that this is indeed the case as far as effort duration and intensity are concerned (e.g. Gendolla & Richter, 2006; Hartmann et al., 2013; Kool et al., 2010; McGuire & Botvinick, 2010; Meyniel, Safra, & Pessiglione, 2014; Porat, Hassin-Baer, Cohen, Markus, & Tomer, 2014; Sugiwaka & Okouchi, 2004), there is very little discussion about the effects of the type of effort (mental or physical) on effort-based decision-making. This is particularly problematic as across the studies examining effort-based decision-making there is an implicit assumption that mental and physical effort are processed in a similar way. Also there is an assumption that mechanisms associated with one type of effort will be observed when the other type of effort is examined as well (e.g. Anzak, Tan, Pogosyan, & Brown, 2011; Boksem & Tops, 2008; Botvinick et al., 2009; Eisenberger, 1992). Without direct comparisons of effort-based decision-making when effort required is either mental or physical this assumption still remains an empirical question.

Looking to the existing literature, the general picture is mixed. For example, mental and physical effort have been found to work in an additive way, whereby expending one type of effort reduces the resources available for the other type of effort. Marcora, Staiano, and Manning (2009) showed that when participants were asked to cycle to exhaustion 90 minutes after a cognitively demanding task, they took less time to reach the exhaustion point compared to participants who were asked to cycle after watching an emotionally neutral movie. The authors interpret this difference as resulting from greater perception of effort in the cognitive demand group, suggesting that mental and physical effort might be processed in an additive way, so that expending one type of effort has consequences for the other type of effort. Nevertheless, it is hard to know whether a different physical task following an earlier cognitive task would generate the same effects.

In contrast, reward discounting in response to mental and physical effort have been found to be well described by similar mathematical models. Ostaszewski, Bąbel, and Swebodziński (2013) investigated mental and physical effort discounting process using a self-report questionnaire. They found that both mental and physical effort discounting were best described by a hyperbolic model, where high rewards were discounted less steeply than small rewards. The steepness of mental and physical effort discounting curves was positively correlated in this study. Nevertheless, Ostaszewski et al. (2013) used hypothetical effort scenarios and hypothetical monetary rewards; this limits the generalizability of their findings to genuine situations of effort with real rewards, such as the studies included in this thesis.

Moreover, Pas et al. (2014) examined the markers of striatal dopaminergic functioning (error-related negativity and eye-blink rate) during mental and physical effort in the presence of subliminal and supraliminal rewards. They found a correlation between mental effort and error-related negativity and physical effort and eye-blink rate during subliminal reward trials. They have taken these findings to suggest that the neurotransmitter dopamine plays a role in the processing of both mental and physical effort. However, as different markers were used for mental and physical effort, the two tasks could not be compared directly, and therefore the conclusions that can be drawn from the study are limited.

In contrast, there are some studies that suggest that mental and physical effort processing might differ, since these two types of effort are processed by distinct brain circuitries (Hosking et al., 2014; Schmidt et al., 2012). For example, Schmidt et al. (2012) tested participants on a task which required detecting numerically greater number within pairs (mental effort) which would determine the hand with which to squeeze a joystick (physical effort). Using fMRI, they observed differential brain activation for mental and physical effort during effort exertion. However, they also found activation in the ventral striatum which drove behaviour during both types of effort, suggesting a role for this structure as a common motivational centre for mental and physical effort.

Therefore, despite the widespread assumption that mental and physical effort is processed similarly, direct comparisons of behaviour during exertion of these two types of effort are rare. Furthermore, of the evidence that exists, the story is rather mixed. To increase our understanding of the effects of mental and physical effort on the Valuation stage, and consequently on effort-based choice and execution, in this thesis performance on mental and physical effort trials will be directly compared empirically. Based on the assumptions of previous effort-based decision-making models, it is hypothesised that mental and physical effort will have the same effect on choice and execution across studies.

2.3 Importance of effort/reward during Action Selection and Action Execution

The V-E-D-M model also makes assumptions about the influence of effort and reward on the Action Selection and Action Execution stages. Many of the decision-making models described in the previous chapter assume that both the Action Selection and Action Execution stages of decision-making are driven by the value of expected rewards. Indeed, substantial evidence exists to suggest that rewards do influence the choices that people make (e.g. Bonnelle et al., 2014; Hartmann et al., 2013; Kool et al., 2010; Treadway et al., 2009) as well as how much effort people exert when trying to obtain a reward (Bijleveld et al., 2009, 2010, 2011, 2012; Bijleveld et al., 2014; Krebs et al., 2012; Le Bouc & Pessiglione, 2013; Marien et al., 2014; Pas et al., 2014; Pessiglione et al., 2007; Zedelius et al., 2011). Nevertheless, alternative conceptualizations of forces driving effort exertion, such as the Theory of Motivation by Brehm and Self (1989), suggest that behaviour during effort-based decision-making might not be driven by rewards, but rather by task demands, for which there is empirical support (e.g. Gendolla et al., 2012; Richter et al., 2008; Richter & Gendolla, 2006; Smith et al., 1990; R. A. Wright, 1984, 1996; R. A. Wright & Kirby, 2001). Therefore, the question as to whether Action Selection and Action Execution are driven by reward or effort is still an open one.

Evidence showing that rewards have a strong impact on effort-based choice and execution is abundant. In general, when people are faced with a task in which they have to decide if they want to put in a particular level of effort for a particular reward, increasing the monetary reward leads to an increase in the level of effort participants are willing to exert (Bonnelle et al., 2014; Hartmann et al., 2013; Kool et al., 2010; Treadway et al., 2009). Rewards are also thought to have a strong effect on effort exertion during Action Execution, as people have been shown to put in more effort (e.g. respond faster or move more vigorously) when the reward they want to obtain is high as compared to low (Bijleveld et al., 2009, 2010, 2011, 2012; Bijleveld et al., 2014; Krebs et al., 2012; Le Bouc & Pessiglione, 2013; Marien et al., 2014; Pas et al., 2014; Pessiglione et al., 2007; Zedelius et al., 2011).

However, in spite of the large number of studies supporting the claim that rewards drive effort-based choice and execution, some evidence exists to suggest that the relationship between effort and reward is not as straightforward. For example, effort has been found to drive choices independently of reward, with participants in most studies preferring the low effort options, regardless of the value of reward associated with them (e.g. Burke et al., 2013;

Kurniawan et al., 2010; Waugh & Gotlib, 2008). Similarly, people have been found to be willing to modulate their effort exertion in response to task requirements in the absence of rewards (e.g. Barnes, Bullmore, & Suckling, 2009; Boehler et al., 2011; Fu et al., 2002; Kool et al., 2010). The results of these studies suggest that rewards might not necessarily drive effort-based choice and execution in all circumstances. These findings are in line with the Theory of Motivation by Brehm and Self (1989), which suggests that effort exertion during a task is guided by task demands, rather than the value of rewards.

Theory of Motivation by Brehm and Self (1989) states that effort exerted during a task should be proportional to task difficulty, rather than rewards at stake, as long as success is possible and reward is deemed to be worth the effort required (see also Gendolla et al., 2012). At the same time, effort should be low if success is impossible or the task is perceived to be too demanding given the rewards it provides. Brehm and Self (1989) acknowledge that rewards have a capacity to influence effort, but they suggest that in most cases reward affects exertion of effort indirectly via setting the maximum amount of effort that should be exerted for a particular reward – the *potential motivation*. One exception is a situation in which a reward is proportional to effort exertion (i.e. the more effort is put in, the higher the reward that is obtained), where effort exerted should increase in line with the value of reward, up to a highest effort level that is possible and justified.

Strong support for this theory comes from studies which use cardiovascular activity (e.g. systolic blood pressure) as a measure of effort exertion (e.g. Gendolla et al., 2012; Richter et al., 2008; Richter & Gendolla, 2006; Smith et al., 1990; R. A. Wright, 1984, 1996; R. A. Wright & Kirby, 2001). For example, Richter et al. (2008) asked participants to perform memory tasks of different levels of difficulty while their heart rate and blood pressure were being assessed. They found that cardiovascular reactivity of participants increased with task difficulty but dropped when the task was impossible to complete. R. A. Wright et al. (1998) made a similar observation when they asked participants to perform five cognitive tasks of different levels of difficulty. They found that cardiovascular reactivity increased with task difficulty for the first three levels of difficulty, and then dropped for the two highest levels of difficulty.

Studies using other measures of effort exertion also provide support for Brehm and Self (1989) Theory of Motivation. For example, Roets, Van Hiel, Cornelis, and Soetens (2008) asked participants to identify a number presented on a screen for variable amounts of time.

Participants could view the number repeatedly by pressing a button on a keyboard. It was found that button pressing (effort) increased as the presentation time decreased, up to a point when observing the number was deemed to be impossible, at which point button pressing decreased. Furthermore, when Prevost et al. (2010) examined willingness to exert effort to view pleasurable erotic stimuli, they found that the value of rewards strongly influenced the choice for costly rewarding options at the intermediate, but not high, levels of effort. Waugh and Gotlib (2008), used a task in which participants had to choose between more and less rewarding options requiring different levels of effort. They demonstrated that, as the effort requirement increased, participants' preference for the reward no longer predicted their choice to work for the reward. The authors have taken this evidence to suggest that as effort increased participants increasingly made their choices based on the level of effort required rather than the rewards at stake.

Considering the strong support for the theory of motivation by Brehm and Self (1989), it is possible that behaviour during Action Selection and Action Execution is mostly driven by assessment of effort requirements. However, there are also many studies which show that behaviour during Action Selection and Action Execution might be driven by rewards. Therefore, it is difficult to determine what actually drives behaviour during these two stages based on the evidence currently available. One of the aims of this thesis is to investigate whether there are potential differences in the effects of reward and effort on the Action Selection and Action Execution stages. If effort-based choices and effort exertion are driven by rewards, reward values should predict participants' behaviour during Action Selection and Action Execution. If, however, they are driven by task demands, behaviour during Action Selection and Action Execution should depend mostly on the effort level required.

2.4 Outcome feedback

The V-E-D-M model assumes that outcome feedback plays an important role when assessing the effects of effort exertion, but this assumption is yet to be verified. Participants of the studies investigating effort-based decision-making conducted so far typically received one of three different types of information at the end of a trial, depending on the study: 1) accuracy feedback (simple outcome feedback, e.g. Kool et al., 2010; Negrotti, Secchi, & Gentilucci, 2005), 2) accuracy feedback + information about reward achieved on a particular trial (discreet feedback, e.g. Capa et al., 2011; Zenon, Sidibe, & Olivier, 2014), or 3) accuracy feedback + reward achieved on a particular trial + cumulative rewards obtained so far (cumulative feedback, e.g. Bijleveld et al., 2009; Bijleveld et al., 2014). Even though the type of feedback used was not discussed in these studies, suggesting that it was not assumed to influence behaviour, these three types of feedback have previously been found to have differing influences on task performance in other tasks, such as complex decision making tasks (Osman, 2011). It is possible that presenting cumulative feedback (accuracy feedback + reward achieved on a particular trial + cumulative rewards) is more motivating than the other two types of feedback. It might lead people to select more effortful options because they are working towards maximizing their gains, which they can see more easily through full feedback information than simple trial by trial information. It is, therefore, important to investigate whether presenting different types of feedback has differing effects on effort-based decision-making behaviour. Consequently, one of the objectives of this thesis is to empirically examine if there are any differences between the effects of simple, discreet, and cumulative feedback on effort-based task performance. In line with the assumptions of the V-E-D-M model it is hypothesised that some differences will be observed. Full cumulative reward feedback is predicted to lead to an increased willingness to choose and execute effortful options, compared to the less comprehensive discreet feedback. The lowest preference for highly effortful options is expected in the simple feedback condition, when no reward information is provided.

2.5 Delayed Action Execution

According to the V-E-D-M model, after the outcome of performed action is evaluated, the discrepancy between the predicted and the actual outcome is used to update the representations of the option that was chosen. The process of learning from the outcome is thought to have a substantial influence on future decisions. One of the implications of this assumption is that preventing people from learning about the outcomes of their decisions should have an impact on their subsequent choices and the amount of effort they exert during a task. However, this assumption has not yet been verified, possibly because investigating this assumption is not as straightforward as it might seem when effort based decision-making is concerned. This is mainly because part of the outcome evaluation during effort-based decision-making involves assessing actual effort exerted during the task, and how this is related to the effort that was anticipated before the task was executed. For this reason simply removing reward feedback from the end of each trial, after effort has been exerted, would not prevent Outcome Evaluation and Learning from happening, as participants would still be updating their effort representations. Therefore, in order to investigate the effect of learning on effort-based decision-making it is necessary to separate choice from the execution stage. This was done in a study by Soman (1998), who examined behaviour in situations in which people had to evaluate options associated with delayed rewards contingent on future effort exertion. He observed that when there was a delay between choice and effort execution, effort required was systematically underweighted, which lead to increased attractiveness of options associated with delayed effort exertion. This means that making decisions in situations in which Action Execution is delayed should lead to underweighting of effort and therefore increased preferences for high effort trials. Nevertheless, further investigations are needed to confirm if this is indeed the case. Therefore, in the present thesis, one of the aims is to investigate effort-based decision-making when execution of the choice is immediate and when it is delayed. Based on the results of the previous studies, it is hypothesised that immediate experience of outcomes will have an influence on effort-based choices and execution, increasing participants' willingness to choose effortful actions.

2.6 Neural underpinnings

Another issue that needs to be explored in the context of V-E-D-M model is the role of dopamine during different stages of effort-based decision-making. The V-E-D-M model is based on the work from neuropsychological and neurobiological studies investigating effort processing in humans and animals. These studies point to an important role for the ACC, the basal ganglia, and the neurotransmitter dopamine in effort-based decision-making (e.g. Bardgett, Depenbrock, Downs, Points, & Green, 2009; Botvinick et al., 2009; Cousins, Atherton, Turner, & Salamone, 1996; Cousins & Salamone, 1994; Croxson et al., 2009; Endepols et al., 2010; Gepshtein et al., 2014; Kroemer et al., 2014; Kurniawan et al., 2013; Kurniawan, Guitart-Masip, & Dolan, 2011; Kurniawan et al., 2010; Ostlund, Wassum, Murphy, Balleine, & Maidment, 2011; Porat et al., 2014; Treadway et al., 2012). Based on the results of these studies, the V-E-D-M model assumes that dopamine plays a role in effort processing during all of the stages identified in the model. However, this assumption still needs to be further verified in humans.

Studies examining effort-based decision-making in humans and animals suggest that the neurotransmitter dopamine plays an important role in decision-making. Midbrain dopamine has been shown to be involved in a) encoding stimuli associated with potential future rewards and losses during representation (e.g. Brooks & Berns, 2013; Phillips, Walton, & Jhou, 2007; Salamone & Correa, 2012), b) representing the reward value discounted by effort costs during the valuation stage (e.g. Prevost et al., 2010), c) overcoming the response costs and energizing ongoing actions during Action Execution (e.g. Berridge & Robinson, 1998; Kurniawan et al., 2013; Niv, Daw, Joel, & Dayan, 2007; Pasquereau & Turner, 2013; Salamone & Correa, 2002; Salamone, Correa, Farrar, & Mingote, 2007), and d) encoding reward prediction error during Outcome Evaluation (e.g. Kable & Glimcher, 2009; Schultz, 1998, 2000, 2002, 2007, 2010; Schultz et al., 1993; Schultz et al., 1997; Schultz & Dickinson, 2000). Most of the information about the role of dopamine in effort-based decision-making in humans comes from studies investigating effort processing in PD patients, which show depletion of dopamine in the midbrain regions.

Studies comparing performance of PD patients and healthy controls (HCs) on effort-based tasks suggest that dopamine is indeed crucial for this process. For example, Mazzoni et al. (2007) examined cost/benefit analysis in PD by comparing arm reaching movements of PD patients and HCs on a speed-accuracy trade-off task. Participants were required to make movements to a target until they reached the criterion of 20 accurate movements within the required speed range. PD patients were found to be as accurate as HCs on this task, however, they took significantly longer to reach criterion on trials that required greater effort (i.e. greater accuracy and faster speed of movement). Mazzoni et al. (2007) hypothesised that this was due to a shift in the cost/benefit analysis in PD patients, which lead them to perceive movements as more effortful.

Further support for this hypothesis comes from a recent study by Chong et al. (2015). They examined the willingness to exert effort for rewards in 26 PD patients ON and OFF dopaminergic medication. This manipulation is of obvious interest because it allows for examination of the contribution of restored dopamine levels to effort-based decision-making. In their task participants were required to put in physical effort (squeeze a hand-grip device) to maximize rewards obtained. Before each trial participants were presented with information about the amount of effort required (as defined by the percentage of their maximum grip strength) and the amount of potential reward available. They had to decide whether to engage in the task or not. The study found that PD patients were less willing to exert effort than healthy controls when the rewards were low, regardless of their medication status. Nevertheless, dopamine was found to have a motivating effect on behaviour, as PD patients chose to invest more effort for a given reward when they were ON dopaminergic medication, as compared to when they were OFF medication.

Other PD studies suggest that dopamine is not only important for cost/benefit analysis during valuation, but also for invigorating effort exertion during Action Execution. Support for this hypothesis comes from a study by Negrotti et al. (2005) which compared the kinematics of reaching movements in PD patients at the early stage and at the later stage of the disease, and in HCs. Negrotti et al. (2005) observed slowing of the velocity parameter of movement in PD patients at the more advanced stages of the disease, but not early in the disease, suggesting an important role of dopamine in determining effort put in a task. Furthermore, Porat et al. (2014) found reduced effort on a task which required PD patients OFF medication to exert physical effort to increase their gain or to avoid loss. This reduction in effort correlated with the degree of dopamine depletion indexed by the severity of the motor symptoms, confirming an important role of dopamine in overcoming effort cost.

Detrimental effects of altered dopamine transmission on effort-based decision-making have been observed in PD patients both when they were tested ON dopaminergic medication (e.g. Majsak, Kaminski, Gentile, & Flanagan, 1998; Mazzoni et al., 2007; Moisello et al., 2011; Negrotti et al., 2005), and when they were tested OFF medication (e.g. Baraduc et al., 2013; Gepshtein et al., 2014; Jokinen et al., 2013; Negrotti et al., 2005; Schneider, 2007; Weingartner, Burns, Diebel, & LeWitt, 1984), suggesting that even a small imbalance in dopamine levels can lead to altered effort processing during effort-based decision-making.

Taken together, the results of the experiments described above suggest that patients with PD are more sensitive to effort requirements and consequently show higher effort discounting during the valuation stage (Mazzoni et al., 2007), which leads to reduced willingness to choose effortful actions. They also suggest that reduced movement speed in PD patients is a product of reduced ability to energize behaviour, which affects the Action Execution stage (e.g. Clery-Melin et al., 2011). Therefore, it seems that investigating effort-based decision-making in PD patients can provide important information about the role of dopamine during different stages of decision making as defined by V-E-D-M model. Consequently, another aim of the empirical work in this thesis is to compare performance of PD patients and HCs on an effort-based decision-making task in order to investigate the effects of altered dopamine transmission on this process.

2.7 Summary

V-E-D-M model makes certain assumptions about effort-based decision-making. It assumes that:

1) Manipulating reward magnitude, reward valence, and reward reliability has an impact on the Valuation stage, and therefore potentially on the whole decision-making process;

2) Manipulating effort type (i.e. whether it is mental or physical) also influences the Valuation stage;

3) Action Selection and Action Execution can be driven either by the rewards available during a decision-making scenario, or by the effort required to obtain them;

4) Feedback following Action Execution plays an important role in Outcome Evaluation;

5) Delaying Action Execution affects effort-based decision-making;

6) Dopamine plays an important role during effort-based decision-making.

The main issue regarding these assumptions is that no evidence is available to support them. Based on the studies conducted so far it is impossible to establish if manipulating different characteristics of effort, reward, and task structure has any effects on the stages of the effort-based decision-making, and what these effects might be. Since V-E-D-M makes certain assumptions regarding these manipulations, the validity of this model cannot be established without investigating these topics first. Thus, to investigate the validity of the V-E-D-M model this thesis concentrated on examining the following hypotheses, based on the studies conducted so far:

H1: Increasing relative as well as absolute reward magnitudes should increase willingness to choose and execute effort on an effort-based decision-making task.

H2: Participants experiencing losses should be less likely to choose effortful trials during the Action Selection stage, and more likely to exert effort during the Action Execution stage.

H3: There should be a positive relationship between the probability of obtaining rewards and the willingness to choose and exert effort.

H4: Mental and physical effort should be processed in the same way during effort-based decision-making.

H5: If behaviour during Action Selection and Action Execution is driven by reward values, it is anticipated that participants' choices and effort exerted should depend primarily on the reward values. If, however, they are driven by effort requirements, we expect choices and effort expenditure to depend mostly on the effort level.

H6: Type of feedback present during a task should have an influence on effort-based choices and actions. Cumulative reward feedback should lead to an increased willingness to choose and execute effortful options, compared to the less comprehensive discreet feedback. The lowest preference for effortful options is expected in the simple feedback condition, when no reward information is provided.

H7: Delayed experience of outcomes should have an influence on effort-based choices. Participants experiencing delayed execution should show increased willingness to choose effortful options compared to participants executing actions immediately after choice.

H8: Depletion of dopamine levels in PD should be associated with decreased willingness to choose and execute effort.

In this thesis, the hypotheses described above are investigated using a novel effort-based decision-making task. Chapter 3 focuses on the design of this task as well as the methods used to analyse the data obtained from this task.

CHAPTER 3: General Methods

The V-E-D-M model makes several assumptions regarding six proposed stages of effort-based decision-making, including assumptions about the effects of manipulating aspects of effort and reward on Valuation, Action Selection, Action Execution, Outcome Evaluation and Learning. In Chapter 2 evidence was reviewed, but there are gaps in the literature which suggest that many of the assumptions the V-E-D-M model may still need empirical qualification. This is because there is no existing work to support or challenge them, either way. In an attempt to address this, the six experiments that were set up as part of this thesis were designed to test the following eight hypotheses:

H1: Participants should show greater willingness to choose and execute effort when rewards are high.

H2: Participants experiencing losses should be less likely to choose effortful trials during the Action Selection stage, and more likely to exert effort during the Action Execution stage.

H3: There should be a positive relationship between the probability of obtaining rewards and the willingness to choose and exert effort.

H4: Mental and physical effort should be processed in the same way during effort-based decision-making.

H5: If behaviour during Action Selection and Action Execution is driven by reward values, it is anticipated that participants' choices and effort exerted should depend primarily on the reward values. If, however, they are driven by task demands, we expect choices and effort expenditure to depend mostly on the effort level required.

H6: Type of feedback present during a task should influence effort-based choices and actions. Full cumulative reward feedback should lead to an increased willingness to choose and execute effortful options compared to the less comprehensive discreet feedback. The lowest preference for effortful options is expected in the simple feedback condition, when no reward information is provided.

H7: Delayed experience of outcomes should have an influence on effort-based choices. Participants experiencing delayed execution should show increased willingness to choose effortful options compared to participants executing actions immediately after choice.

H8: Depletion of dopamine levels in PD should be associated with decreased willingness to choose and execute effort in this group.

The present chapter is divided into three sections. The first one describes the methods used in previous studies of effort-based decision-making, which served as the basis for the design of the experimental procedures used in the six experiments of this thesis. The second section describes in detail the actual experimental procedure that was used. The final section describes the types of analyses that were conducted on the data obtained from the experiments presented in this thesis. In the following Chapters 4, 5 and 6 the results of the experimental manipulations described in this chapter are reported. This format of presentation (i.e. chapter describing the general methods used, followed by three chapters concentrating purely on results) was chosen to achieve maximum clarity as to what the findings of each individual study mean in the context of the assumptions of the V-E-D-M model. Since the model separates the Action Selection and Action Execution stages, in this thesis the results relating to these two stages are presented separately. In Chapter 4 the results from the Choice phase (representing Action Selection) of each experiment are discussed. In Chapters 5 and 6 the results from the Execution phase (representing Action Execution) are described. Chapter 5 concentrates on effort exertion during Action Execution, whereas Chapter 6 describes results relating to the accuracy of performance during this stage.

3.1 Methods used to investigate effort-based decision-making

Effort-based decision-making has been examined using a variety of methods. Studies investigating the effect of effort on choice and execution focused on identifying brain networks involved in effort processing and investigating the consequences of disruption to these networks (e.g. Croxson et al., 2009; Kroemer et al., 2014; Kurniawan et al., 2013; Kurniawan et al., 2010; Le Bouc & Pessiglione, 2013), as well as investigating the effects of effort and reward on effort-based decision-making (e.g. Anzak et al., 2011; Bijleveld et al., 2009, 2010, 2011, 2012; Bonnelle et al., 2014; Hartmann et al., 2013; Meyniel et al., 2014). The next section of this chapter provides an overview of different methodologies used in these studies, which served as a basis for devising the task used in the investigation of the V-E-D-M model proposed in this thesis. Investigations of mental and physical effort have used different methodologies, and for that reason they are described in separate subsections.

3.1.1 Mental effort

Mental effort has most commonly been investigated using tasks which require increased concentration and sustained attention, and/or put a great load on working memory. An example of a task requiring sustained attention is a *parity judgement task*. In this task participants need to assess if a number appearing on a computer screen is odd/even, or if it is bigger or smaller than another specified number. Effort in this task is manipulated by changing the number of times participants need to switch from assessing parity to assessing magnitude, and it is measured using response times and accuracy of responding. The more switches are required, the more effortful the task is considered to be, which is indexed by measuring response times (which increase) and accuracy (which decreases) (Botvinick et al., 2009; Botvinick & Rosen, 2009; Kool et al., 2010; McGuire & Botvinick, 2010).

Another popular paradigm used in the investigations of mental effort is the *n-back working memory task*. In this task participants are presented with series of stimuli appearing on a screen one by one, and are required to recall if they saw a particular stimulus *n* presentations previously (e.g. Barnes et al., 2009; Eubanks et al., 2002; Kool & Botvinick, 2014; Otto, Zijlstra, & Goebel, 2014; Satterthwaite et al., 2012; Westbrook et al., 2013). In this case effortfulness is determined by *n*, and can be measured using cardiovascular responses (e.g. Eubanks et al., 2002), accuracy of responding (e.g. Kool & Botvinick, 2014), or self-report measures of effort (e.g. Otto et al., 2014). The higher the *n* number is, the more effortful the task is considered to be. In turn, this is associated with increased cardiovascular activations, decreased accuracy, and increased subjective ratings of effort.

Alternatively, many studies investigating mental effort present participants with *maths problems*. Typically, they involve solving equations appearing on a computer screen (e.g. Bijleveld et al., 2010; Hernandez Lallement et al., 2014; Jokinen et al., 2013). Here effortfulness is determined by the number of equations that need to be solved under a deadline or by their difficulty, and is measured by response times and accuracy. In general, in the tasks that used this method, response times increased and accuracy decreased in line with increasing effort requirements.

An important feature of the paradigms described above is that for each one effort can be measured using multiple and varied methods, and this depends on the research questions being asked in the studies. Mental effort has been assessed using measures that include self-report and questionnaires (e.g. Efklides, Kourkoulou, Mitsiou, & Ziliaskopoulou, 2006;

Ostaszewski et al., 2013; Roets et al., 2008), response times (e.g. Jokinen et al., 2013; Kool et al., 2010; Marien et al., 2014; Pas et al., 2014), pupil dilation (e.g. Bijleveld et al., 2009; Boehler et al., 2011), and cardiovascular responses (e.g. Eubanks et al., 2002; Gendolla & Krüsken, 2001, 2002; Gendolla & Richter, 2005; Richter et al., 2008; Smith et al., 1990; Smith, Nealey, Kircher, & Limon, 1997; R. A. Wright, 1984, 1996). What this suggests is that currently there is no accepted or standardized measure of mental effort exertion. This makes it harder to assess across studies what types of mental effort tasks have greater impact on mental effort exertion. It also makes it hard to assess how mental effort impacts different stages of the effort-decision-making process. Only broad conclusions can be drawn which suggest that when the difficulty of a mental task is manipulated, or the time available to complete it is manipulated, then accuracy is affected, along with other measures. However, there is no way of knowing which measure is the most appropriate for gauging mental effort.

3.1.2 Physical effort

The situation seems to be a bit better with regard to examining physical effort. This is because tasks used to elicit physical effort typically adopt the same paradigm, which involves a hand grip device. These tasks measure the grip strength with which participants squeeze a joystick in response to stimuli presented on a computer screen (e.g. Anzak et al., 2011; Anzak et al., 2012; Bonnelle et al., 2014; Burke et al., 2013; Chong et al., 2015; Hartmann et al., 2013; Kurniawan et al., 2013; Kurniawan et al., 2010; Meyniel et al., 2014; Meyniel et al., 2013; Pessiglione et al., 2007; Prevost et al., 2010; Schmidt et al., 2009; Schmidt et al., 2008; Zenon et al., 2014). Thus, across all these studies grip strength is considered to be the index of effort exertion such that the stronger the grip, the more effort is presumed to be exerted.

Outside of the typical hand grip paradigm, several studies have measured physical effort using other hand movements, such as reaching movements. For example, in some studies participants were required to move their hand to a target with a particular speed and accuracy in response to external stimuli (Baraduc et al., 2013; Majsak et al., 1998; Mazzoni et al., 2007; Moisello et al., 2011; Montgomery & Nuessen, 1990; Negrotti et al., 2005). The higher the speed and accuracy requirements, the more effortful the task was considered to be. In these tasks effort exerted was thought to be reflected by the speed of movement that was performed (Baraduc et al., 2013; Majsak et al., 1998; Moisello et al., 2011; Montgomery & Nuessen, 1990), and/or its accuracy (Majsak et al., 1998; Montgomery & Nuessen, 1990). In addition, physical effort has been measured more simply by examining button presses on a computer keyboard (most often with the little finger), or clicking a computer mouse in response to stimuli presented on screen (Bijleveld et al., 2012; E. D. Klein et al., 2005; Kroemer et al., 2014; Pas et al., 2014; Porat et al., 2014; Treadway et al., 2012; Treadway et al., 2009; Wardle, Treadway, & de Wit, 2012; Wardle, Treadway, Mayo, Zald, & de Wit, 2011). Here, effort was shown to increase as indexed by the number of button presses (i.e. finger tapping speed) (Bijleveld et al., 2012; Pas et al., 2014), or the number of mouse clicks (Kroemer et al., 2014; Porat et al., 2014).

As with mental effort, in physical effort tasks effort has been measured using a variety of methods. While the hand grip paradigm is the most popular, certainly in most recent research history on physical effort, the methods by which effort is measured are broad. Methods of measurement of effort can include self-report questionnaires (e.g. Sugiwaka & Okouchi, 2004), pupil dilation (e.g. Zenon et al., 2014), duration of movement (e.g. Samuels & Whitecotton, 2011; Sprinkle, 2000), speed of movement (e.g. Ballanger et al., 2006; Baraduc et al., 2013; Croxson et al., 2009; Pas et al., 2014), movement velocity (e.g. Majsak et al., 1998; Moisello et al., 2011), reaction time (e.g. Kojovic et al., 2014; Kurniawan et al., 2013), grip strength (e.g. Anzak et al., 2011; Anzak et al., 2012; Bonnelle et al., 2014; Burke et al., 2013; Chong et al., 2015), and number of responses (e.g. button presses) (Porat et al., 2014; Venugopalan et al., 2011). Many of the issues that were raised regarding mental effort also apply to the study of physical effort. There is no agreed measure of physical effort, and no way to align the different ways in which physical effort is manipulated and measured in order to assess which physical effort tasks are most effortful, and how that impacts on decision-making behaviour.

3.1.3 Mental and physical effort

Of concern to a number of literatures is the assumption that the underlying basis on which mental and physical effort based decisions are made is in fact the same. However, this assumption is hard to validate empirically because so few studies actually directly compare the two. Of the work reviewed the only measure that seems to have been used consistently to examine effort exertion in both mental and physical effort tasks is accuracy. It is generally assumed that increased effort exertion should translate into increased task performance, as reflected by improved accuracy. This indeed has been observed in several studies examining mental as well as physical effort (e.g. Bijleveld et al., 2010; Kurniawan et al., 2013; Pas et al., 2014; Schmidt et al., 2012). Of course, these studies use different incentive schemes in which the rewards are presented in different ways, with different feedback, and as discussed in the previous chapter, the interaction between rewards and effort exertion is not straightforward. Nevertheless, in the literature reviewed, it does appear that when people commit to greater effort exertion this usually corresponds to increases in performance accuracy.

As discussed, different methodologies used to examine effort-based decision-making described above limit the extent to which inferences can be drawn about the types of tasks that lead to greater effort. Furthermore, inconsistencies in the designs across the different studies reviewed also mean that the results of these studies are difficult to compare, and potential differences between them are difficult to interpret. This is particularly problematic when mental and physical effort are concerned, as there is an implicit assumption that these two types of effort are processed in the same way. Vast discrepancies between the tasks used to investigate mental and physical effort mean that this assumption cannot really be supported. Therefore, it seems that this area of research would strongly benefit from a more consistent approach in terms of the methodologies used. This would allow for direct comparisons between tasks, which should lead to a better understanding of effort-based decision-making in mental and physical tasks.

3.1.4 Present experimental paradigm

The present experimental set up used in the six experiments presented in this thesis is novel. However, attempts were made so that it was compatible with the designs of previous studies investigating mental and physical effort–based decision-making. In each of the six experiments mental effort was measured using a mental arithmetic task, where difficulty was determined by the number of equations appearing on the screen and measured by recording response times as well as accuracy. Increased effort exertion in this task was indexed by an elevation in response times and increased accuracy. For physical effort the hand grip paradigm was used. Grip strength and accuracy were used as the indicators of effort exertion, in line with previous studies of this type. Additionally, the choices participants made regarding the amount of effort they were willing to exert for different levels of reward were also recorded for both mental and physical effort. The goal of designing this task was to investigate the eight hypotheses described at the beginning of this chapter, to establish the validity of the assumptions made by the V-E-D-M model. These hypotheses were investigated in six experiments. The exact hypotheses investigated in each experiment are presented in Table 2.

In all six experiments the same effort-based decision-making task was used and three types of measures were recorded: 1) choices made, 2) behavioural measures of effort exertion (i.e. grip strength for physical effort and response times for mental effort), and 3) accuracy of performance. These three types of measures were investigated in relation to the eight hypotheses described above. For the clarity of presentation and interpretation in terms of the assumptions of the model, the results of the six experiments are presented together for each type of dependent measure in Chapters 4, 5, and 6. The remaining part of this chapter describes the methods of data collection and data analysis in the six experiments described above.

Table 2. Hypotheses investigated in the six experiments forming the empirical part of this thesis

Experiment	Hypotheses							
	H1 Effects of manipulating reward magnitude	**H2** Effects of manipulating reward valence	**H3** Effects of manipulating reward reliability	**H4** Comparison of mental/physical effort	**H5** Reward/Effort driving behaviour	**H6** Effects of manipulating reward feedback	**H7** Effects of immediate/delayed execution	**H8** Effects of dopamine depletion
Experiment 1 (Gains)	+			+	+	+		
Experiment 2 (Losses)	+	+		+	+			
Experiment 3 (Reliability)	+		+	+	+			
Experiment 4 (Increased Incentives)	+		+	+	+			
Experiment 5 (Immediate Execution)	+			+	+	+	+	
Experiment 6 (PD study)	+			+	+			+

3.2 Methods

3.2.1 Participants

In total, 222 participants were recruited for the six experiments. Participants in Experiments 1, 2, 3, 4 and 5 were recruited using a research volunteers' contact list from Queen Mary University of London. Participants for Experiment 6 were recruited from the movement disorders clinic at the National Hospital for Neurology and Neurosurgery.

1) Forty two participants (23 males) were recruited for **Experiment 1 (Gains)**. As one participant was found to be unable to complete the mental effort trials, their data were removed from the analysis. The mean age of the remaining participants was 20.56 (*SD*=2.46). Participants were assigned randomly to each of the feedback conditions: Cumulative (*N*=13), Discreet (*N*=14), and Simple (*N*=14).

2) Forty five participants (12 males) were recruited for **Experiment 2 (Losses)**. Mean age of the participants was 20.58 (*SD*=1.08). Participants were assigned randomly to each of the feedback conditions: Cumulative (*N*=15), Discreet (*N*=15), and Simple (*N*=15).

3) Forty two participants (7 males) were recruited for **Experiment 3 (Reliability)**. Mean age of the participants was 22.07 (*SD*=5.37). Participants were assigned randomly to each of the reward reliability conditions: Deterministic (*N*=15), Probabilistic (*N*=14), and Random (*N*=13).

4) Thirty participants (4 males) were recruited for **Experiment 4 (Increased Incentives)**. Mean age of the participants was 21.77 (*SD*=7.54). Participants were assigned randomly to each of the reward reliability conditions: Deterministic (*N*=10), Probabilistic (*N*=10), and Random (*N*=10).

5) Thirty two participants (5 males) were recruited for **Experiment 5 (Immediate Execution)**. Mean age of the participants was 20.78 (*SD*=3.73). Participants were assigned randomly to each of the feedback conditions: Cumulative (*N*=11), Discreet (*N*=11), and Simple (*N*=10).

6) Thirty one participants were recruited for **Experiment 6 (PD study).** Two participants (one PD patient and one HC) were not able to complete mental effort trials, and had to be removed from the analysis. Data from 15 PD patients (12 males), aged between 42 and 79 (*M*=64.73, *SD*=10.29), and 14 HCs (6 males) aged between 37 and 83 (*M*=71.43, *SD*=11.32)

was included in the analysis. Mean duration of illness in the PD group was 6 years (*SD*=5.15). All patients were non-demented, as demonstrated by scores above 24 on the Mini-Mental State Examination (MMSE) (Folstein, Folstein, & McHugh, 1975). Screening for depression using the Beck Depression Inventory-II (BDI-II) (Beck, Steer, & Brown, 1996) revealed 4 PD patients scored in the depressed range (score >18). One patient had a clinical diagnosis of depression and was taking antidepressant medication at the time of the study. However, removing their data from the analysis was not found to significantly change the results and therefore it was included in the final analysis. Stage of illness was assessed using the Hoehn and Yahr scale (Hoehn & Yahr, 1998). Disability was assessed with the Schwab and England Activities of Daily Living scale (Schwab & England, 1969). All patients where in the mild to moderate stages of the disease with scores on the Hoehn and Yahr scale ranging from 1 to 4 (M=1.98, SD=0.90). On the Schwab and England scale scores ranged from 5 to 9 (M=7.84, SD=1.02). All patients were examined while on dopaminergic medication. Mean levodopa equivalent dose was 566.50 mg (*SD*=327.30). Levodopa equivalent dose, duration of illness, and disease severity as measured by Hoehn and Yahr (1998) were not correlated with participants' performance during the task.

3.2.2 Materials

Participants in all six experiments completed a version of a newly developed computerized effort-based decision-making task designed specifically for this thesis. The task was programed using Matlab 2012a with Psychtoolbox 3 extension and presented to participants on a 19'' monitor using an IBM computer. Participants' role during the task was to exert mental effort (solve simple mathematical equations) and physical effort (squeeze a hand grip device) to obtain small monetary rewards. The amount of effort required (High or Low) and the amount reward to be won (High or Low) differed between trials. The exact structure of the task differed between experiments, depending on the manipulations they included. The summary of different manipulations introduced in the six experiments is presented in Table 3 and described in sections 3.2.2.1 – 3.2.2.4 of this chapter. Participants' responses were recorded using a standard keyboard (mental effort) and a grip force transducer (physical effort) forming a part of fORP 932 Subject Response Package, developed by Cambridge Research Systems. The maximum grip strength measured by the transducer was 100N on a scale from 0 to 35000. The task consisted of three stages: Training phase, Choice phase and Execution phase. The Training phase was formed of 16 trials, and Choice and Execution phases consisted of 48 trials (Experiments 1-5) or 60 trials (Experiment 6). The visual layout of each phase is presented in Figure 2.

On each Training and Execution trial a thermometer was presented in the centre of the screen, with the reward information displayed on top. The thermometer was divided into three sections by three horizontal lines in equal distance from each other. Other elements presented on the screen depended on the Effort Type (Mental vs. Physical), Effort Level (High vs. Low), and Reward Level (High vs. Low) on a particular trial. Duration of each trial was 4.5s (Experiments 1-5) or 6s (Experiment 6). After each trial participants received feedback which included information about the financial outcome of this trial. This feedback depended on the Feedback condition participants were assigned to (Cumulative/Discreet/Simple in Experiments 1-3, Deterministic/Probabilistic/Random in Experiments 4-5, Discreet in Experiment 6). The following section describes Effort Type, Effort Level, Reward Level, and Feedback manipulations in more detail.

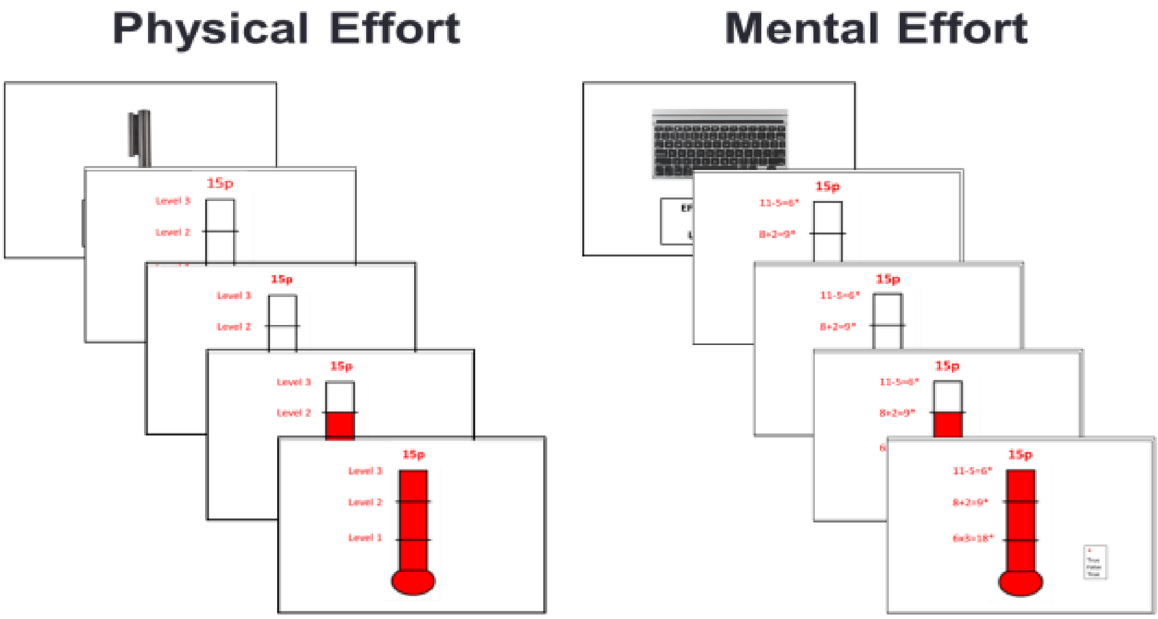


Figure 2. Visual layout of the novel effort-based decision-making task

Table 3. Summary of manipulations and changes to the task introduced in different experiments

Experiment	Structure	
	Manipulations	Changes from Baseline (Experiment 1)
Experiment 1 (Gains)	Effort Level, Reward Level, Reward Feedback	
Experiment 2 (Losses)	Effort Level, Reward Level, Reward Valence, Reward Feedback	**Reward Valence manipulation**: 2 groups - *Gain* and *Loss* . *Loss* group: given £6.40 at the beginning of the Execution phase. Avoided lossing 5p on LS trials or 15p on HS trials. *Gain* group: as in Experiment 1
Experiment 3 (Reliability)	Effort Level, Reward Level, Reward Reliability	**Reward Reliability manipulation**: 3 groups - *Deterministic*, *Probabilistic* , and *Unreliable* . *Deterministic* : received rewards on 100% of successful trials; *Probabilistic* : received rewards on 75% of successful trials and 25% of unsuccessful trials; *Unreliable* :received rewards on 50% of the trials, regardless of whether they were successful or not. No Reward Feedback manipulation
Experiment 4 (Increased Incentives)	Effort Level, Reward Level, Reward Reliability, Reward Magnitude	**Reward Magnitude manipulation:** 2 groups *Large Rewards* and *Small Rewards* . *Small Rewards* : received 5p on LR trials and 15p on HR trials; *Large Rewards* : received 15p on LR trials and 30p on HR trials. In addition: Reward Reliability manipulation. No Reward Feedback manipulation
Experiment 5 (Immediate Execution)	Effort Level, Reward Level, Timing of Execution, Reward Feedback	**Timing of Execution manipulation:** 2 groups - *Immediate Execution* and *Delayed Execution* . *Immediate Execution* : Choice and Execution phases were combined into one. Participants had to exert effort straight after making their decision. *Delayed Execution* : Choice and Execution phases were separated. Participants made all their decisions first, and then they had to execute them.
Experiment 6 (PD study)	Effort Level, Reward Level, Group	**Group manipulation:** 2 groups - *PD patients* and *HCs*. No Reward Feedback manipulation. Additional changes were introduced to adjust the task to the specific needs of PD patients and older HCs: Grip strength calibration, prolonging of trial length, task was self-paced. Additional type of trial was added (No Effort No Reward -NENR trial), to encourage participants to select HELR trials on some occasions. Including additional trials resulted in the increase in the total number of Choice and Execution trials from 48 to 60.

3.2.2.1 Effort Type manipulation

Mental Effort

During the mental effort trials simple mathematical equations (e.g. 2+4=6 or 5+3=7) appeared on the left hand side of the thermometer next to the dividing lines. Participants' role was to indicate if an equation was solved correctly or not by pressing an appropriate button (Experiments 1-5: 'z' and 'm'; Experiment 6: 'n' and 'm' respectively) on the keyboard. Participants had to solve all the equations appearing on the screen to successfully complete a trial. Each equation consisted of three one digit numbers forming either an addition, subtraction or a multiplication which were already solved. Half of the total number of equations presented to participants during the experiment was solved incorrectly. Difference between the correct answer and the incorrect answer presented on the screen was within the ±3 range. Correct and incorrect equations were distributed randomly between trials.

Physical Effort

During the physical effort trials signs indicating the level of effort to be achieved (e.g. 'Level 1', 'Level 3') appeared on the left hand side of the thermometer. Participants had to squeeze the joystick with an appropriate strength to successfully complete a trial.

3.2.2.2 Effort Level manipulation

High Effort (HE)

During the high mental effort trials participants had to solve three equations appearing on the screen. In Experiments 1-5 during the high physical effort trials participants had to squeeze the joystick with the strength above 75% of maximum grip strength that could reliably be measured by the transducer, which represents the force of 75 Newtons. All participants were capable of achieving this force. In Experiment 6 participants had to squeeze the joystick with the strength above 60% of their maximum grip strength; this was measured before the actual experiment began.

Low Effort (LE)

During the low mental effort trials participants had to solve one equation. During the low physical effort trials participants had to squeeze the joystick with the strength above 15% of the maximum grip strength that could reliably be measured by the transducer (Experiments 1-5), which represented the force of 15 Newtons. In Experiment 6 participants had to squeeze the joystick with the strength above 15% of maximum grip strength, as measured before the experiment started.

In Experiments 1-5 participants had to solve all of the equations appearing on the screen within 4.5s or maintain their grip above the threshold level for 4.5s to successfully complete both High and Low Effort trials. Each trial terminated after 4.5s, regardless of whether it was successful or not. In Experiment 6 the length of each trial was extended to 6s, to accommodate for potentially longer response times in PD patients.

3.2.2.3 Reward Level manipulation

On the *High Reward* (HR) trials the amount of reward presented on top of the thermometer was 15p. On the *Low Reward* (LR) trials the amount of reward presented was 5p (Experiments 1, 3, 5 and 6). In Experiment 2 (Losses), participants were first endowed with £6.40, which coincided with the maximum amount that could be won in Experiment 1. Their goal was to avoid losing this money. In this experiment, the amount presented on *High Stake* (HS) trials was -15p, and the amount presented on *Low Stake* (LS) trials was -5p. In Experiment 4 (Increased Incentives) these rewards were doubled, so that participants were presented with 30p on High Reward trials and 10p on Low Reward trials.

3.2.2.4 Reward Feedback manipulation

After each trial participants received general performance feedback and reward information which differed depending on the condition they were assigned to (Cumulative, Discreet, or Simple in Experiments 1, 2 and 5; Deterministic, Probabilistic, Random in Experiments 3-4).

3.2.2.4.1 Experiments 1, 2 and 5

Cumulative condition

In the Cumulative condition participants received information about whether they had successfully completed the trial (‘Good job’/’Not this time’), how much money they would have won (Training) or actually won (Execution) on this particular trial, and how much money they have accumulated so far.

Discreet condition

In the Discreet condition participants received information about whether they had successfully completed the trial (‘Good job’/’Not this time’), and how much money they would have won (Training) or actually won (Execution) on this particular trial. This was also the only type of feedback available for participants in Experiment 6.

Simple condition

In the Simple condition participants received information only about whether they had successfully completed a trial (‘Good job’/’Not this time’). No information about rewards was presented.

3.2.2.4.2 Experiments 3 and 4

After each trial participants received feedback, which informed them if they had successfully obtained the reward (‘Good job’ vs. ‘Not this time’) and how much money they would have won (Training phase) or actually won (Execution phase) on this particular trial.

Deterministic condition

In the Deterministic condition, successful completion of a trial resulted in positive feedback (‘Good job’) and acquisition of reward. Unsuccessful trial received ‘Not this time’ feedback.

Probabilistic condition

In the Probabilistic condition, successful completion of a trial resulted in positive feedback (‘Good job’) and acquisition of reward on approximately 75% of the trials. Unsuccessful trials would result in positive feedback and acquisition of reward on 25% of the trials, otherwise the rest of the time an unsuccessful trial received ‘Not this time’ feedback.

Unreliable condition

In the Unreliable condition, each trial was associated with a 50% probability of experiencing positive feedback (‘Good job’) and obtaining a reward, regardless of whether it was completed successfully or not, otherwise the rest of the time a trial received ‘Not this time’ feedback.

3.2.3 Procedure

The visual layout of the screen, cover story and instructions were identical for Experiments 1-6. Participants were informed that they would be required to exert mental and physical effort to obtain small monetary rewards (Experiments 1 and 3-6) or to avoid losing money that was given to them at the beginning of the experiment (Experiment 2). They were also told that they would be able to choose between different combinations of effort and reward before they would be required to put in effort. The exact phases participants were asked to go through are presented in Figure 3.

The experiment began with a short demonstration during which participants had a chance to familiarize themselves with the visual characteristics of the task and practice using the joystick. Since the maximum grip strength that could be measured by the joystick (i.e. 100N) was greatly below average maximum grip strength for males (approx. 420N) and females (approx. 240N) as reported by Mathiowetz et al. (1985), no calibration of the device was conducted, as it was assumed that all participants were capable of achieving the grip strength thresholds required in this task. This assumption was confirmed by the experimenter for each participant on an individual basis during the short initial demonstration. In Experiment 6, calibration of the joystick was conducted, however, to account for the weaker grip strength observed in the older people, and PD patients in particular (Bohannon, Bear-Lehman, Desrosiers, Massy-Westropp, & Mathiowetz, 2007; Corcos, Chen, Quinn, McAuley, & Rothwell, 1996). Calibration was done through asking participants to squeeze the joystick as hard as they could three times in a row. The highest measurement was taken to represent participants' maximum grip strength. Demonstration/calibration was followed by the Training phase, consisting of 16 trials, during which participants experienced different levels of effort and reward.

Training phase was designed to familiarize participants with the effort demands and the reward structure of the task. No monetary rewards were awarded at this stage. Each training trial started with a screen informing participants about the type of effort required. Participants saw either a picture of the joystick which indicated physical effort, or a picture of a keyboard which indicated mental effort. Below the picture there was an information about the level of effort required and about the level of associated reward (even though no actual rewards were handed out at this stage) on the following trial. There were four possible effort/reward combinations: high effort high reward (HEHR), high effort low reward (HELR), low effort high reward (LEHR) and low effort low reward (LELR). This information appeared on the screen for 3s. Next, a thermometer was presented in the centre of the screen, with the reward information displayed on top.

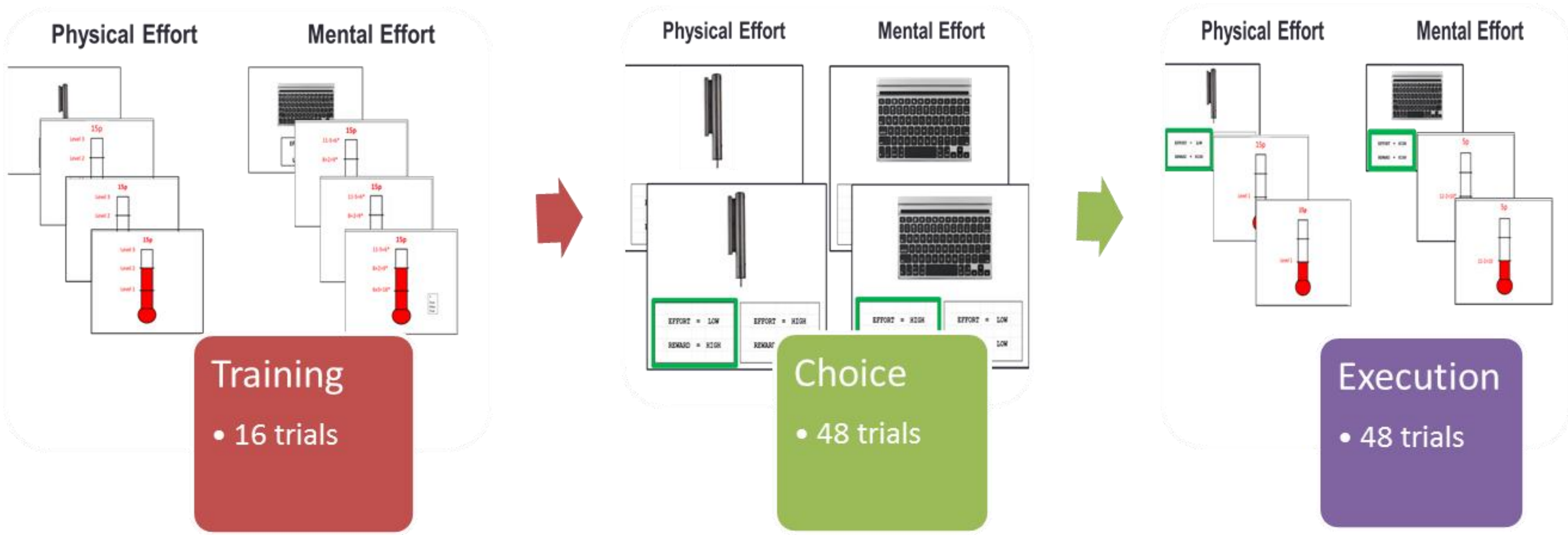


Figure 3. Outline of the three different phases of the effort-based decision-making task

On mental effort trials, after each successful response the level of the mercury in the thermometer would go up. After an incorrect response the trial would terminate. On physical effort trials maintaining the squeeze caused the level of the mercury in the thermometer to go up. Loosening the grip strength below a predefined threshold level resulted in a termination of the trial. Each type of effort/reward combination (HEHR, HELR, LEHR, LELR) appeared twice during the training phase for each effort type (Mental vs. Physical). The order of presentation was randomized.

Training phase was followed by the Choice phase, during which participants had to repeatedly choose between two options presented on the screen by pressing an appropriate button on the keyboard. Mental and physical effort options were presented in an alternate manner. Choice phase was designed to investigate the choices participants made when deciding about exerting effort for rewards. In this phase on each consecutive trial participants saw a picture of a keyboard or a picture of a joystick appearing on the screen, representing mental or physical effort respectively. Underneath the picture two options were displayed. The two options differed in terms of the level of effort required, level of reward to be obtained, or both. Each combination of possible options (HEHR vs HELR vs LEHR vs LELR) appeared on the screen four times in a random order. Participants made their choice by pressing an appropriate button on the keyboard, after which the chosen option would be highlighted in green and the trial would terminate. Participants had an unlimited time to make their decision. Participants' choices determined what trials participants' encountered in the Execution phase. The Choice phase consisted of 48 (Experiments 1-5) or 60 (Experiment 6) trials. In Experiment 3 (Immediate Execution) each choice was immediately followed by an execution trial. In the other experiments participants made 48/60 choices first, one after another, and only after all the choices were made they were transferred to the Execution phase

In the Execution phase (Experiments 1-4 and 6) participants were first reminded of their choice and then they had to execute it by either squeezing the joystick or solving the equations appearing on the screen. Each successfully completed trial increased participant's final win. Execution trials were presented in the same order as the choice trials. In Experiment 5 (Immediate Execution) there was no need to remind participants about their choice before the trial started, as execution trials followed choice trials straight away.

3.3 Data analysis

Statistical package R v. 3.1.1 (R Core Team, 2014) was used to analyse the data. Grip strength and response times measurements from both correct and incorrect trials were averaged for the four different types of trials (HEHR, HELR, LEHR, LELR). Response times were trimmed: those shorter than 150ms (Experiments 1-5) or 200ms (Experiment 6) and longer than 4.5s (Experiments 1-5) or 6s (Experiment 6) were excluded from the analysis, so that the data analysed would be contained in the middle 95% of the distribution, in line with the methods commonly used to deal with reaction time outliers, as described by Ratcliff (1993) and Whelan (2010).

As the Training phase was used only to familiarise participants with the task environment, and consisted of only two trials of each type (i.e. 2x HEHR, 2x HELR, 2x LEHR, 2x LELR) data from this phase was not included in the analyses described in the following sections.

Preliminary analyses of the choice, effort exertion, and accuracy data gathered in the six experiments revealed that the number of observations (available data points) was not even across conditions and experiments. Furthermore, diagnostic procedures forming part of initial mixed ANOVA analysis of the effort execution data showed that in some instances the residuals (i.e. the differences between observed values and the values estimated by the ANOVA model) were not normally distributed. These factors, in addition to the fact that choice and accuracy data was categorical, meant that mixed ANOVA design was not an appropriate method of data analysis. For that reason linear mixed models (LMMs) and generalized linear mixed models (GLMMs), appropriate for dealing with unbalanced designs (Bolker et al., 2009; Faraway, 2005, 2014) were used to analyse the data. Package 'lme4' was used for the modelling purposes (Bates, Maechler, Bolker, & Walker, 2014).

Experiment 1 (Gains) was used as a baseline for Experiments 2 (Losses) and 5 (Immediate Execution). Similarly, Experiment 3 (Reliability) was used as a baseline to which Experiment 4 (Increased Incentives) was compared. Experiment 6 (PD study) was analysed separately, as the design of this experiment differed slightly from the other five.

3.3.1 Model specification

Fixed and random factors included in the models used for the analysis of the data from the six experiments are presented in Table 4.

Dependent variables analysed in this thesis were: Choice, Grip Strength (physical effort only), Response Times (mental effort only), and Accuracy. Choice represented the number of times each option was chosen when it was available. Grip strength was the measurement obtained from the hand grip device. Response times represented the time it took participants to solve all of the equations appearing on the screen within the 4.5s (or 6s in the case of Experiment 6) deadline. Accuracy reflected the number of trials completed successfully by participants.

In Experiment 2 during Choice analysis ‘Attractiveness’ (High vs. Low) of an option was entered as a factor into the analysis instead of Reward. Options involving high reward (+15p) or low loss (-5p) were coded as High in attractiveness, whereas options involving low reward (+5p) or high loss (-15p) were coded as Low in attractiveness. In the same experiment, during the analysis of behavioural measures and accuracy ‘Stake’ (High vs. Low) was entered into the analysis instead of Reward. High Stake represented trials during which participant could win or lose 15p, whereas Low Stake represented trials during which participants could win or lose 5p.

Analyses of physical and mental effort data were conducted separately, due to the differences in methods used to elicit mental and physical effort. In addition, choices made during physical and mental effort trials, as well as accuracy on mental and physical effort trials were compared in separate analyses for each experiment. These analyses included Effort Type, as well as the main experimental manipulations described in Table 4 as fixed factors, and Subject ID as a random factor.

For post hoc analyses Tukey HSD test was used as a method of adjusting *p* values for multiple comparisons.

Table 4. Fixed and random factors included in the models in different experiments

Experiment	Model Specification	
	Fixed Factors	Random Factors
Experiment 1 (Gains)	**Effort Level** (High vs. Low), **Reward Level** (High vs. Low), **Reward Feedback** (Cumulative/Discreet/Simple)	Participant ID
Experiment 2 (Losses)	**Effort Level** (High vs. Low), **Stake/Attractiveness Level** (High vs. Low), **Reward Valance** (Gain vs. Loss), **Reward Feedback** (Cumulative/Discreet/Simple)	Participant ID
Experiment 3 (Reliability)	**Effort Level** (High vs. Low), **Reward Level** (High vs. Low), **Reward Reliability** (Deterministic/Probabilistic/Unreliable),	Participant ID
Experiment 4 (Increased Incentives)	**Effort Level** (High vs. Low), **Reward Level** (High vs. Low), **Reward Magnitude** (Large Rewards vs. Small Rewards), **Reward Reliability** (Deterministic/Probabilistic/Unreliable),	Participant ID
Experiment 5 (Immediate Execution)	**Effort Level** (High vs. Low), **Reward Level** (High vs. Low), **Timing of Execution** (Immediate Execution vs. Delayed Execution), **Reward Feedback** (Cumulative/Discreet/Simple)	Participant ID
Experiment 6 (PD study)	**Effort Level** (High vs. Low), **Reward Level** (High vs. Low), **Group** (PD vs. HC)	Participant ID

Choice and Accuracy were categorical variables, and so were investigated using GLMMs assuming binomial distribution, appropriate for the analysis of counts data (Bolker et al., 2009). Grip strength and RT data was examined using LMMs, appropriate for the analysis of continuous data, assuming that residuals are normally distributed (Bolker et al., 2009). As the residuals in the case of RT data were found not to be normally distributed, and no data transformation alleviated this problem, GLMMs assuming gamma distribution with logarithmic or inverse link were used to analyse this data (Bolker et al., 2009)

Backward method of variable selection was used to create models of different complexity. Information theoretic tool (AIC) was used to select the models with the highest estimated predictive power (Bolker et al., 2009). Based on this criterion the final models were selected in each Experiment. The exact models selected in each experiment are described in Appendix A.

3.3.2 Model diagnostics, parameter estimation and model selection

For LMMs, the assumptions of normality and homogeneity of variance were examined by visual inspection of residual plots and by using Shapiro-Wilk test of normality (Faraway, 2014). If these assumptions were violated, data was transformed to normality using appropriate transformations. In the case of grip strength data, square root transformations of reversed scores were typically used (see Appendix A). As far as response times are concerned, this data could not be transformed to normality using standard transformations, and so GLMMs assuming gamma or inverse distributions were used for the analysis (see Appendix A).

For GLMMs assuming gamma or inverse distributions residual plots were examined to make sure the assumption of homogeneity of variance was not violated (Faraway, 2005). No residual plots indicated violation of this assumption.

For GLMMs assuming binomial distribution the ratio between the sum of squared Pearson residuals and the residual degrees of freedom was analysed to check for overdispertion (Faraway, 2005). When this assumption was violated a random factor for each observation was included in the model.

Maximum Likelihood method was used to estimate the parameters of each model. Likelihood ratio test was used to test fixed effects (Bolker et al., 2009).

The exact details of how each model was created can be found in Appendix A.

3.4 Summary

In previous investigations of effort-based decision-making described in Chapters 1 and 2 various methods of effort measurement were used. Among these measures response times, grip strength and accuracy proved to be the most popular. Therefore, to achieve consistency with previous investigations, these three methods of effort measurement were used in a newly developed effort-based decision-making task designed to investigate the eight hypotheses derived from the V-E-D-M, described in Chapter 2. The task consisted of three phases: Training phase, Choice phase, and Execution Phase. During the Training and Execution phases participants were required to squeeze a hand grip device (physical effort) or solve simple mathematical equations appearing on the screen (mental effort) to obtain small monetary rewards. During the Choice phase participants were required to choose between options associated with different levels of effort and reward. Different aspects of this task were manipulated in the six experiments designed to investigate the hypotheses forming the focus of this thesis. Data gathered during these experiments was then analysed using LMMs and GLMMs. The results of these analyses are presented in the next three chapters, describing the effects of experimental manipulations on the choices people made (Chapter 4), effort they exerted (Chapter 5), and accuracy they achieved (Chapter 6). Such format was chosen to achieve maximum clarity regarding the implications of the findings from the six experiments for the assumptions of the V-E-D-M model.

CHAPTER 4: Experimental Studies - Choice

The V-E-D-M model makes various assumptions regarding effort and reward processing during six different stages of effort-based decision-making. For example, it assumes that manipulating reward magnitude/valence/reliability or effort type should affect choices people make during an effort-based decision-making task. Moreover, it stipulates that changing the feedback structure or preventing learning during decision-making should also have an impact on choices. These assumptions have not been verified, however. Therefore, in this chapter the effects of manipulating the aspects of the decision-making problem described above on the choices participants made in a newly developed effort-based decision-making task were investigated. The specific areas covered by these investigations were: 1) **Reward manipulations**, 2) **Effort manipulations**, 3) **Importance of effort/reward during Action Selection and Action Execution**, 4) **Outcome feedback**, 5) **Delayed Action Execution**, and 6) **Neural underpinnings**, as specified in Chapter 2.

As far as **Reward manipulations** are concerned, in this chapter the effects of a) increasing relative as well as absolute reward values, b) changing reward valence (from gain to loss), and c) changing reward reliability on participants' choices were examined. Furthermore, participants' choices on mental and physical effort trials wer compared, to investigate the effects of **Effort manipulations**. **Importance of effort/reward during Action Selection** was also explored through investigating participants' preferences when options associated with different levels of effort and reward were available. The effects of different types of **Outcome feedback,** as well as the effects of **Delaying Action Execution** on participants' choices were examined as well. Finally, the role of dopamine during Action Selection stage was investigated, in an effort to explore the **Neural underpinnings** of effort-based decision-making.

These topics were investigated in six studies which used the novel effort-based decision-making task described in Chapter 3. This task consisted of three phases: Training phase, Choice phase, and Execution phase (see Figure 3). This chapter focuses specifically on participants' performance during the Choice phase. During this phase participants were repeatedly presented with two out of four possible options associated with different levels of effort and reward (HEHR vs. HELR vs. LEHR vs. LELR) and were required to choose the option that they wanted to execute (see Figure 4). Participants' choices were analysed using binomial GLMM. The results of these analyses are presented in this chapter.

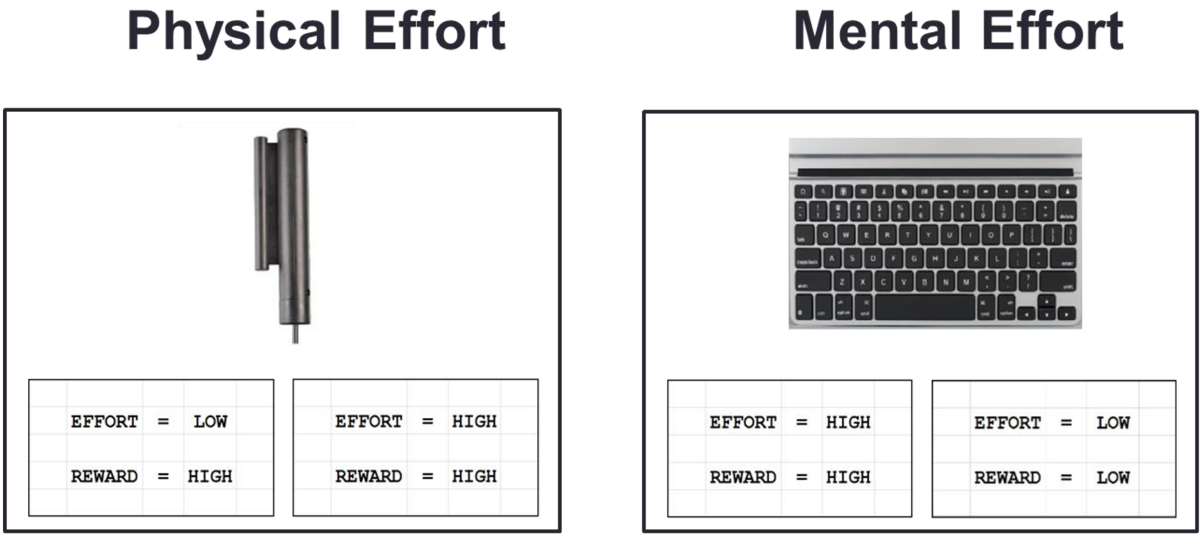


Figure 4. Example of choices participants faced during the effort-based decision-making task

Eight specific hypotheses regarding the effects of manipulating effort, reward, and feedback structure on the choices people make were investigated:

H1: Increasing incentives available in a task should increase participants' willingness to choose high effort options.

H2: Participants trying to avoid losing monetary rewards should choose low effort options more often than participants trying to win monetary rewards.

H3: Positive relationship between the probability of obtaining rewards and the willingness to choose high effort options should be observed.

H4: Choices on mental effort trials should not be different from choices on physical effort trials.

H5: If behaviour during Action Selection is driven by reward values, participants should mainly choose high reward options. If, however, it is driven by effort requirements, they should mainly choose low effort options.

H6: Type of feedback present during a task should have an effect on the choices people make. Cumulative reward feedback should lead to an increased willingness to choose high effort options compared to discreet feedback. The lowest preference for high effort options is expected in the simple feedback condition, when no reward information is provided.

H7: Participants experiencing delayed Action Execution should show increased willingness to choose effortful options.

H8: Depletion of dopamine levels in the brain associated with PD should lead to reduced willingness to choose high effort options.

In Chapter 4 the effects of different experimental manipulations on the choices participants made during the task are described and interpreted in the context of the eight hypotheses presented above. Summary of the findings of different experiments is presented in Table 5.

Table 5. Results of the analyses of choices made by participants during six main experiments with regard to the 8 hypotheses investigated. "+" represents hypothesis supported by the results of the experiment, "-" represents hypothesis for which support has not be found, "partial" represents hypothesis for which partial support has been found.

Experiment	**Hypotheses**							
	H1 Effects of manipulating reward magnitude	**H2** Effects of manipulating reward valence	**H3** Effects of manipulating reward reliability	**H4** Comparison of mental/physical effort	**H5** Reward/Effort driving behaviour	**H6** Effects of manipulating reward feedback	**H7** Effects of immediate/delayed execution	**H8** Effects of dopamine depletion
Experiment 1 (Gains)	+			-	reward	-		
Experiment 2 (Losses)	+	+		+	reward			
Experiment 3 (Reliability)	+		partial	+	reward			
Experiment 4 (Increased Incentives)	relative: + absolute -		partial	+	reward			
Experiment 5 (Immediate Execution)	+			-	reward	-	-	
Experiment 6 (PD study)	+			+	reward			-

4.1 Results

In each of the following sections the experimental design is briefly described first, followed by the results from the physical effort trials, mental effort trials, and the comparison of the two types of trials. At the end of each section the findings are discussed in the context of the experimental hypotheses.

Table showing how often each option (HEHR, HELR, LEHR, LELR) was chosen when it was available is included in Appendix B.

4.1.1 Experiment 1 (Gains)

Experiment 1 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on choices associated with either mental or physical effort. Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Selection,

4) H6, which concerns the effects of different types of feedback on choice.

Participants' preferences on mental and physical effort trials in Experiment 1 are presented in Figure 5.

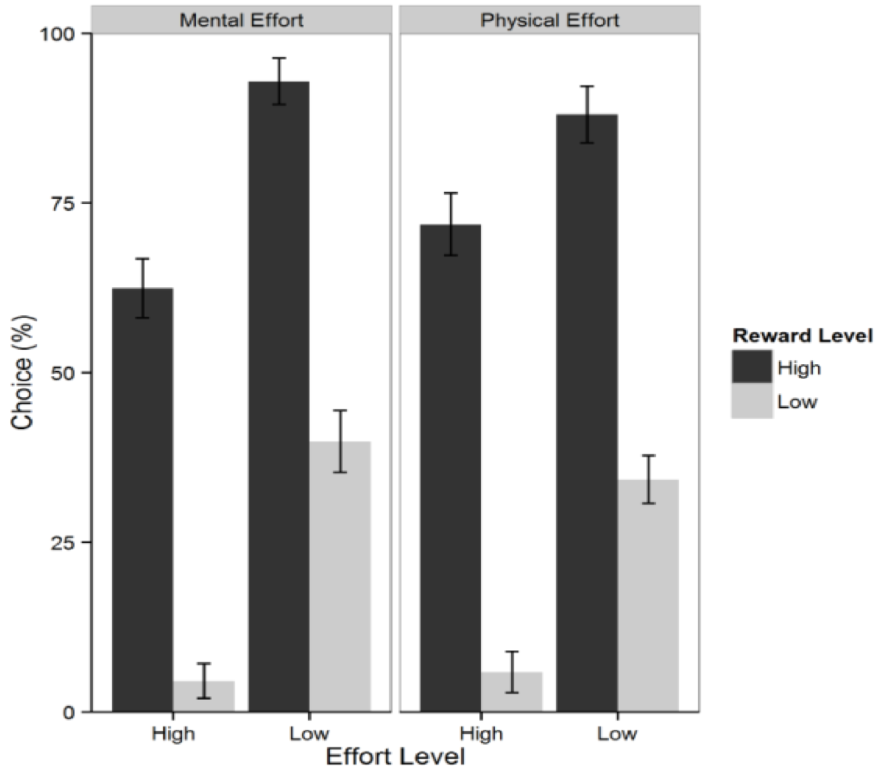


Figure 5. Percentage of times each option was chosen when it was available during mental and physical effort trials in Experiment 1.

Physical Effort

Analysis of choices participants made during physical effort trials revealed significant main effects of Effort Level ($\chi^2(2)=111.23$, $p<.001$) and Reward Level ($\chi^2(2)=259.97$, $p<.001$), as well as an interaction between Effort Level and Reward Level ($\chi^2(1)=13.38$, $p<.001$).

Confirming the pattern indicated in Figure 5, there was an overall preference for Low Effort over High Effort options (β=1.63, *SE*=.15, *z*=10.65, *p*<.001), an overall preference for High Reward over Low Reward options (β=3.29, *SE*=.16, *z*=20.48, *p*<.001), but also an interaction between Effort Level and Reward Level.

Post hoc comparisons using Tukey HSD test showed that participants were more likely to choose LEHR trials over HEHR (β=1.08, *SE*=.19, *z*=5.59, *p*<.001), LELR (β=2.73, *SE*=.19, *z*=14.05, *p*<.001), and HELR trials (β=4.92, *SE*=.27, *z*=18.41, *p*<.001). Furthermore, participants were found to have a preference for HEHR trials over LELR (β=1.65, *SE*=.16, *z*=10.05, *p*<.001) and HELR trials (β=3.84, *SE*=.24, *z*=15.78, *p*<.001). They were also found to choose LELR over HELR trials (β=2.18, *SE*=.23, *z*=9.30, *p*<.001), as indicated by Figure 5.

Mental Effort

Analysis of choices people made during mental effort trials revealed significant main effects of Effort Level ($\chi^2(2)=175.28$, $p<.001$) and Reward Level ($\chi^2(2)=258.78$, $p<.001$).

As suggested by Figure 5, there was an overall preference for Low Effort over High Effort options (β=2.34, *SE*=.17, *z*=14.02, $p<.001$), and an overall preference for High Reward over Low Reward options (β=3.30, *SE*=.17, *z*=19.33, $p<.001$).

Post hoc comparisons using Tukey HSD test showed that participants were more likely to choose LEHR trials over HEHR (β=2.09, *SE*=.21, *z*=9.53, $p<.001$), LELR (β=3.05, *SE*=.22, *z*=13.73, $p<.001$), and HELR trials (β=5.67, *SE*=.30, *z*=18.88, $p<.001$). Furthermore, participants were found to have a preference for HEHR trials over LELR (β=.96, *SE*=.16, *z*=6.13, $p<.001$) and HELR trials (β=3.58, *SE*=.25, *z*=14.32, $p<.001$). They were also more likely to choose LELR over HELR trials (β=2.61, *SE*=.25, *z*=10.58, $p<.001$), as demonstrated in Figure 5.

Physical vs. Mental Effort

Comparison of choices made on mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(2)=13.91$, $p<.001$), as well as a significant interaction between Effort Type and Effort Level ($\chi^2(1)=13.89$, $p<.001$).

Further analyses using Tukey HSD test revealed that participants were less likely to choose High Effort trials (β=-.38, *SE*=.14, *z*=2.69, $p=.04$) when effort required was mental, rather than physical. Participants were also more likely to choose Low Effort trials (β=.35, *SE*=.13, *z*=2.64, $p=.04$) when effort required was mental, as indicated by Figure 5.

Discussion

In general, results of Experiment 1 suggest that: 1) increased reward values lead to increased willingness to choose effortful options, 2) mental and physical effort are processed differently, 3) choices are driven by reward values, and 4) feedback does not have a strong influence on the choices people make.

More specifically, Experiment 1 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H4, H5 and H6. In line with H1, which predicts that increasing relative reward values should lead to increased willingness to choose effortful options, participants were found to be more likely to choose high effort trials if they were associated with high rewards.

Contrary to H4, which asserts that mental and physical effort should be processed in a similar way, the findings also suggest that mental and physical effort might be processed differently during the choice phase, as participants were found to choose low effort options more often on mental effort trials than on physical effort trials. It is, however, hard to determine precisely what is the basis for this difference. Alternative explanations are considered in more detail in the general discussion in Chapter 7.

Another hypothesis examined in this experiment was H5, which predicts that if Action Selection is driven by reward values participants should primarily select trials associated with high rewards. In line with this hypothesis participants were found to have a strong preference towards options associated with high rewards, regardless of whether these options required high or low effort. At the same time participants were found to take effort into account as well, showing a preference for low over high effort options. Nevertheless, effort considerations were found to be less important than reward considerations in this experiment.

Finally, contrary to H6, which states that different types of outcome feedback should affect Action Selection differently, no differences in the choice behaviour were observed between groups receiving different types of feedback, suggesting that feedback might not be as important during choice as assumed by the V-E-D-M model.

4.1.2 Experiment 2 (Losses)

Experiment 2 was a 2 (Effort Level: High vs. Low) x 2 (Attractiveness Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Reward Valence: Gain vs. Loss) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low attractiveness on choices associated with either mental or physical effort in two groups of participants: one trying to win monetary rewards (Gain group: participants from Experiment 1) and one trying to avoid losing them (Loss group). In contrast to Experiment 1, where options associated with high and low rewards were compared, in this experiment the influence of option attractiveness was investigated. In the Gain group High Attractiveness (HA) trials were associated with an opportunity to win 15p and Low Attractiveness (LA) trials with an opportunity to win 5p. In the Loss group HA trials were associated with potential loss of 5p, whereas LA trials were associated with potential loss of 15p. Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H2, which concerns the effects of gains and losses

3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Selection,

5) H6, which concerns the effects of different types of feedback on choice.

Preliminary inspection of the data revealed that participants in the Cumulative feedback condition did not choose the HELA trials at all, and for this reason feedback had to be removed from the analyses, as otherwise the model would not converge due to zero cell counts for categorical predictors.

Participants' preferences on mental and physical effort trials in Experiment 2 are presented in Figure 6.

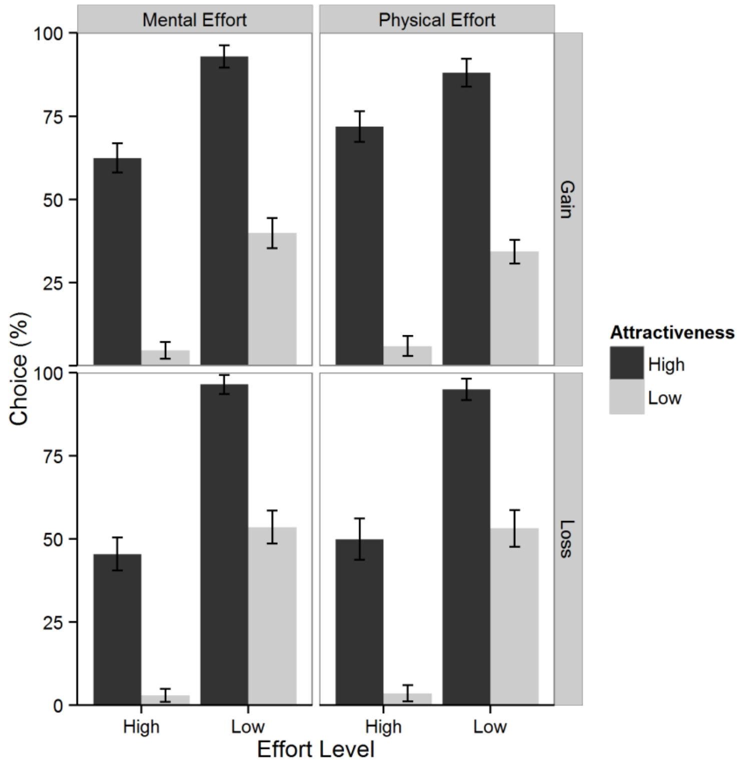


Figure 6. Percentage of times each option was chosen when it was available on mental and physical effort trials in Experiment 2.

Physical effort

Analysis of choices participants made during physical effort trials revealed significant main effects of Effort Level ($\chi^2(3)=362.82$, $p<.001$), Attractiveness ($\chi^2(3)=470.4$, $p<.001$) and Reward Valence ($\chi^2(3)=55.57$, $p<.001$). Interactions between Reward Valence and Effort Level ($\chi^2(1)=44.30$, $p<.001$), and Effort Level and Attractiveness ($\chi^2(1)=11.23$, $p<.001$) were also significant.

In general participants were found to have a preference towards Low Effort trials over High Effort trials ($\beta=2.54$, $SE=.13$, $z=18.94$, $p<.001$). Participants were also found to prefer High Attractiveness trials over Low Attractiveness trials across experiments ($\beta=3.32$, $SE=.14$, $z=24.27$, $p<.001$).

Post hoc comparisons using Tukey HSD test indicated that participants in the Loss group were significantly less likely to choose High Effort trials compared to participants from the Gain group ($\beta=-.85$, $SE=.18$, $z=-4.78$, $p<.001$). At the same time, participants in the Loss group were significantly more likely to choose the Low Effort trials ($\beta=.85$, $SE=.16$, $z=5.24$, $p<.001$). Participants in both Gain ($\beta=1.69$, $SE=.17$, $z=9.84$, $p<.001$) and Loss ($\beta=3.39$, *SE*=.20, *z*=17.18, *p*<.001) groups were shown to prefer Low Effort trials over High Effort trials.

Participants were also found to be more likely to choose LEHA trials over HEHA (β=2.11, *SE*=.17, *z*=12.30, *p*<.001), LELA (β=2.89, *SE*=.17, *z*=16.76, *p*<.001), and HELA trials (β=5.86, *SE*=.24, *z*=24.82, *p*<.001). Furthermore, participants were found to have a preference for HEHA trials over LELA (β=.78, *SE*=.13, *z*=5.89, *p*<.001) and HELA trials (β=3.75, *SE*=.20, *z*=18.75, *p*<.001). They were also more likely to choose LELA over HELA trials (β=2.96, *SE*=.20, *z*=15.05, *p*<.001), as indicated by Figure 6.

Mental Effort

Analysis of choices made by participants on mental effort trials revealed significant main effects of Effort Level (χ^2(3)=463.51, *p*<.001), Attractiveness (χ^2(3)=505.37, *p*<.001), and Reward Valence (χ^2(3)=36.23, *p*<.001). Interaction between Reward Valence and Effort Level (χ^2(1)=25.24, *p*<.001) was also significant.

In general participants were found to have a preference towards Low Effort trials over High Effort trials (β=3.04, *SE*=.14, *z*=22.12, *p*<.001). Participants in both Gain and Loss groups were also found to prefer High Attractiveness trials over Low Attractiveness trials (β=3.36, *SE*=.14, *z*=24.32, *p*<.001).

Post hoc comparisons using Tukey HSD test indicated that participants in the Loss group were less likely to choose High Effort trials (β=-.70, *SE*=.17, *z*=-4.03, *p*<.001) and more likely to choose Low Effort trials (β=.60, *SE*=.16, *z*=3.71, *p*=.001) compared to participants in the Gain group. Participants in both Gain (β=2.39, *SE*=.17, *z*=13.77, *p*<0.001) and Loss (β=3.69, *SE*=.20, *z*=18.05, *p*<.001) groups showed a preference for Low Effort trials over High Effort trials.

Participants were also found to be more likely to choose LEHA trials over HEHA (β=2.84, *SE*=.18, *z*=15.90, *p*<.001), LELA (β=3.16, *SE*=.18, *z*=17.63, *p*<.001), and HELA trials (β=6.40, *SE*=.25, *z*=25.68, *p*<.001). Furthermore, participants were found to have a preference for HEHA over LELA (β=.32, *SE*=.12, *z*=2.73, *p*=.03) and HELA trials (β=3.56, *SE*=.20, *z*=17.84, *p*<.001). They were also more likely to choose LELA over HELA trials (β=3.24, *SE*=.20, *z*=16.27, *p*<.001), as indicated by Figure 6.

Physical vs. Mental effort

Comparison of the choices made on mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(8)=105.12$, $p<.001$), as well as significant interactions between Effort Type and Effort Level ($\chi^2(4)=104.4$, $p<.001$), Effort Type and Valence ($\chi^2(4)=93.23$, $p<.001$), and Effort Type, Valence and Effort Level ($\chi^2(2)=93.00$, $p<.001$). Further analyses, however, revealed no significant differences between choices on mental and physical effort trials, as indicated by Figure 6.

Discussion

In general, the results of Experiment 2 suggest that: 1) increased rewards and/or reduced losses lead to increased willingness to choose effortful options, 2) when losses are a possibility, willingness to choose effortful options is reduced 3) mental and physical effort are processed in the same way, 4) choices are driven by monetary outcomes.

More specifically, Experiment 2 was designed to test four hypotheses derived from the V-E-D-M model and prior literature: H1, H2, H4 and H5. In line with H1, which states that increasing relative reward values should increase participants' willingness to choose effortful options, participants were found to be more likely to choose high effort trials if they were associated with attractive monetary outcomes. This suggests that increasing the financial attractiveness of an effortful option, through increasing the reward or decreasing the loss associated with it, leads to increased likelihood that this option will be chosen.

In accordance with H2, which asserts that participants should be more risk averse in the face of losses, this experiment also showed that participants from the Loss group were more likely to choose low effort options compared to participants from the Gain group, suggesting that effort is processed differently when there is a gain or loss framing.

As far as H4 is concerned, which states that mental and physical effort should be processed in a similar manner, participants' preferences were found to be the same across mental and physical effort trials, in line with this hypothesis.

Furthermore, participants were found to be most likely to choose options characterized by high attractiveness of the monetary outcome, regardless of the amount of effort associated with these options. Therefore, Experiment 2 provides support for H5, which states that reward values, rather than effort requirements, drive choices during Action Selection.

4.1.3 Experiment 3 (Reliability)

Experiment 3 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 3 (Reward Reliability: Deterministic vs. Probabilistic vs. Unreliable) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on choices associated with either mental or physical effort in three groups: Deterministic (reward present on 100% of successful trials), Probabilistic (reward present on 75% of successful trials and 25% of unsuccessful trials), or Unreliable (reward present on 50% of the trials, regardless of whether they were successful or not).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H3, which concerns the effects of reward reliability

3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Selection.

Participants' preferences on mental and physical effort trials in Experiment 3 are presented in Figure 7.

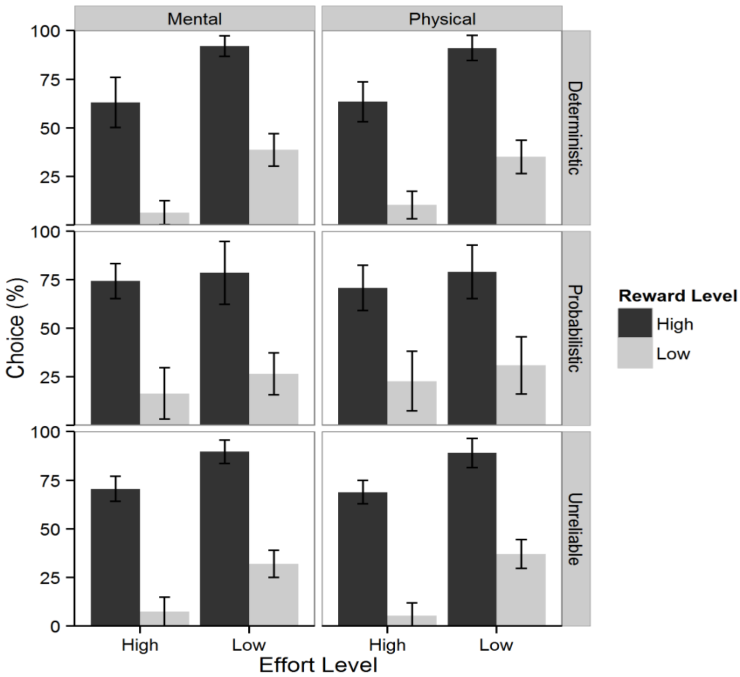


Figure 7. Percentage of times each option was chosen when it was available on mental and physical effort trials in Experiment 3.

Physical effort

Analysis of the choices participants made on physical effort trials revealed significant main effects of Effort Level ($\chi^2(4)=63.50$, $p<.001$), Reward Level ($\chi^2(2)=175.25$, $p<.001$), and Reward Reliability ($\chi^2(4)=10.65$, $p=.03$), as well as a significant interaction between Reward Reliability and Effort Level ($\chi^2(2)=10.48$, $p=.005$).

In general participants were found to prefer Low Effort trials over High Effort trials (β=1.49, *SE*=.20, *z*=7.43, *p*<.001). Participants were also found to choose High Reward trials much more often than Low Reward trials (β=3.09, *SE*=.21, *z*=14.74, *p*<.001).

Post hoc comparisons using Tukey HSD test indicated that participants were more likely to choose Low Effort trials over High Effort trials in the Deterministic (β=1.88, *SE*=.32, *z*=5.74, *p*<.001) and Unreliable (β=1.98, *SE*=.36, *z*=5.53, *p*<.001) conditions, but not in the Probabilistic condition (*p*=.41).

Participants were also found to be more likely to choose LEHR trials over HEHR (β=1.38, *SE*=.28, *z*=4.99, *p*<.001), LELR (β=2.98, *SE*=.28, *z*=10.61, *p*<.001), and HELR trials (β=4.59, *SE*=.33, *z*=14.06, *p*<.001). Furthermore, participants were found to have a preference for HEHR trials over LELR (β=1.60, *SE*=.25, *z*=6.43, *p*<.001) and HELR trials (β=3.21, *SE*=.29, *z*=11.02, *p*<.001). They were also more likely to choose LELR over HELR trials (β=1.60, *SE*=.28, *z*=5.67, *p*<.001), as indicated by Figure 7.

Mental Effort

Analysis of the choices participants made on the mental effort trials revealed significant main effects of Effort Level ($\chi^2(4)=74.64$, $p<.001$), Reward Level ($\chi^2(2)=197.22$, $p<.001$), and Reward Reliability ($\chi^2(4)=13.42$, $p=.009$) as well as a significant interaction between Effort Level and Reward Reliability ($\chi^2(2)=13.40$, $p=.001$).

In general participants were found to prefer Low Effort trials over High Effort trials (β=1.55, *SE*=.20, *z*=7.86, *p*<.001). Participants were also found to choose High Reward trials much more often than Low Reward trials (β=3.29, *SE*=.21, *z*=16.00, *p*<.001).

Post hoc comparisons using Tukey HSD test indicated that participants were more likely to choose Low Effort trials over High Effort trials in the Deterministic (β=2.31, *SE*=.34, *z*=6.87, *p*<.001) and Unreliable (β=1.77, *SE*=.35, *z*=5.09, *p*=.03) conditions, but not in the Probabilistic (*p*=.38) condition.

Participants were also found to be more likely to choose LEHR trials over HEHR (β=1.34, *SE*=.26, *z*=5.07, *p*=<.001), LELR (β=3.07, *SE*=.27, *z*=11.40, *p*<.001), and HELR trials (β=4.86, *SE*=.32, *z*=15.02, *p*<.001). Furthermore, participants were found to have a preference for HEHR trials over LELR (β=1.74, *SE*=.24, *z*=7.38, *p*<.001) and HELR trials (β=3.52, *SE*=.29, *z*=12.25, *p*<.001). They were also more likely to choose LELR over HELR trials (β=1.78, *SE*=.28, *z*=6.35, *p*<.001), as indicated by Figure 7.

Physical vs. Mental effort

Comparison of choices during mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(12)=25.02$, *p*=.01), as well as significant interactions between Effort Type and Effort Level ($\chi^2(6)=24.76$, *p*<.001), Effort Type and Reward Reliability ($\chi^2(8)=23.93$, *p*=.002), and Effort Type, Reward Reliability and Effort Level ($\chi^2(4)=23.76$, *p*<.001). However, further analyses revealed no significant differences between choices made on physical and mental effort trials, as indicated by Figure 7.

Discussion

In general, the results of Experiment 3 suggest that: 1) increased rewards lead to increased willingness to choose effortful options, 2) reward reliability does affect choices, but only when rewards are probabilistic 3) mental and physical effort are processed in the same way, and 4) choices are driven by rewards.

More specifically, in Experiment 3 four hypotheses derived from the V-E-D-M model were investigated: H1, H3, H4, and H5. In line with H1, the results of this experiment suggested that increased incentives lead to increased willingness to choose effortful actions, as participants were found to be more likely to choose high effort trials when they were associated with high rewards.

Results of this experiment do not, however, support H3, which predicted positive relationship between the probability of obtaining rewards and the willingness to choose high effort options. Participants in Experiment 3 were found to be more likely to choose low effort trials over high effort trials when the reward-predicting cues experienced during the Training phase were deterministic, i.e. they reliably predicted the presence of a reward after a successful trial. Participants were also more likely to choose low effort trials compared to high effort trials when rewards experienced during the Training phase were unreliable. When acquisition of reward after effort exertion could not be predicted, however, but a link between effort exertion and reward acquisition could be suspected (i.e. in the Probabilisitic condition where the reasoning might be as follows: ‘I am more likely to get a reward on a successful trial, and I am more likely to be successful when I invest more effort, and so it follows that I should be more likely to get a reward when I invest more effort’), participants were found to choose high and low effort trials equally often.

No differences between choices regarding mental effort and choices regarding physical effort were observed in Experiment 3, in line with H4, which states that these two types of effort should be processed in a similar way.

As far as the question of whether reward values or effort requirements drive Action Selection, (H5) is concerned, the results of this experiment suggest that reward values play a more important role, as participants were found to have a strong preference for high reward trials, regardless of the amount of effort they required.

4.1.4 Experiment 4 (Increased Incentives)

Experiment 4 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Reward Magnitude: Large Rewards vs. Small Rewards) x 3 (Reward Reliability: Deterministic vs. Probabilistic vs. Unreliable) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on choices associated with either mental or physical effort in two groups: one exerting effort for small rewards (15p and 5p) (Small Rewards group: participants from Experiment 3) and one exerting effort for large rewards (30p and 15p) (Large Rewards group). Participants were randomly assigned to one of the three groups: Deterministic (reward present on 100% of successful trials), Probabilistic (reward present on 75% of successful trials and 25% of unsuccessful trials), or Unreliable (reward present on 50% of the trials, regardless of whether they were successful or not).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative as well as absolute reward values and effort,

2) H3, which concerns the effects of reward reliability,

3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Selection.

Participants' preferences on mental and physical effort trials in Experiment 4 are presented in Figure 8.

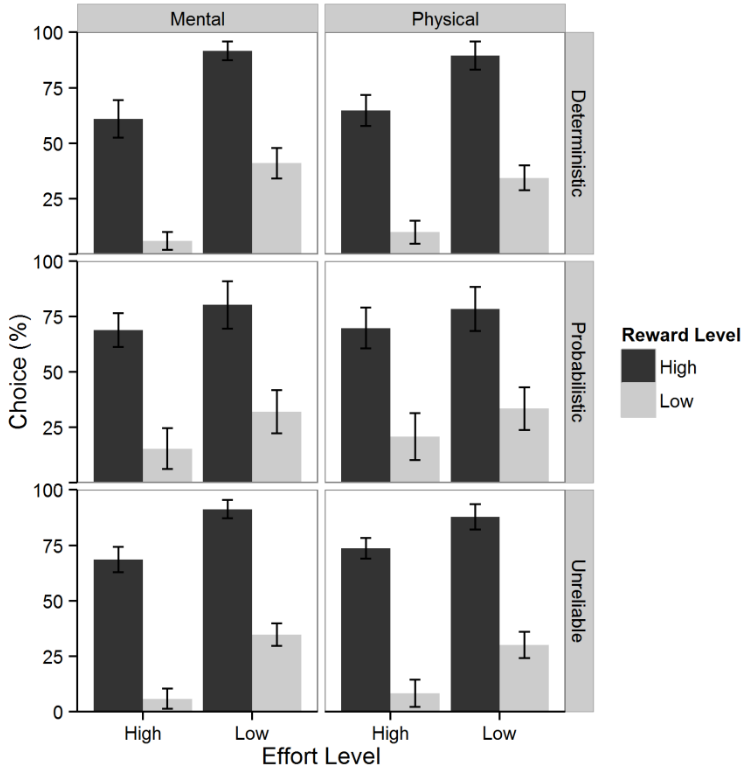


Figure 8. Percentage of times each option was chosen when it was available on mental and physical effort trials in Experiment 4.

Physical effort

Analysis of choices participants made on physical effort trials revealed significant main effects of Effort Level ($\chi^2(4)=88.60$, $p<.001$), Reward Level ($\chi^2(4)=304.40$, $p<.001$), and Reward Reliability ($\chi^2(6)=16.75$, $p=.01$). Interactions between Reward Reliability and Effort Level ($\chi^2(2)=10.23$, $p=.006$) and Reward Reliability and Reward Level ($\chi^2(2)=8.11$, $p=.02$) were also found to be significant.

In general participants were found to prefer Low Effort trials over High Effort trials ($\beta=1.35$, $SE=.15$, $z=8.88$, $p<.001$). Participants were also found to choose High Reward trials much more often than Low Reward trials ($\beta=3.13$, $SE=.16$, $z=19.60$, $p<.001$).

Post hoc comparisons using Tukey HSD test indicated that participants in the Deterministic ($\beta=3.24$, $SE=.26$, $z=12.38$, $p<.001$), Probabilistic ($\beta=2.56$, $SE=.25$, $z=10.19$, $p<.001$), and

Random (β=3.58, *SE*=.28, *z*=12.93, *p*<.001) conditions were significantly more likely to choose the High Reward options over Low Reward options. Participants in the Deterministic (β=1.82, *SE*=.26, *z*=7.03, *p*<.001), Probabilistic (β=.72, *SE*=.25, *z*=2.94, *p*=.04), and Random (β=1.52, *SE*=.27, *z*=5.58, *p*<.001) conditions were also more likely to choose Low Effort trials over High Effort trials.

Participants were also found to be more likely to choose LEHR trials over HEHR (β=1.19, *SE*=.21, *z*=5.67, *p*<.001), LELR (β=2.96, *SE*=.21, *z*=13.89, *p*<.001), and HELR trials (β=4.48, *SE*=.25, *z*=18.18, *p*<.001). Furthermore, participants were found to have a preference for HEHR trials over LELR (β=1.77, *SE*=.19, *z*=9.25, *p*<.001) and HELR trials (β=3.29, *SE*=.22, *z*=14.84, *p*<.001). They were also more likely to choose LELR over HELR trials (β=1.52, *SE*=.22, *z*=7.06, *p*<.001), as indicated by Figure 8.

Mental effort

Analysis of participants choices during mental effort trials revealed significant main effects of Effort Level (χ^2(7)=156.62, *p*<.001), Reward Level (χ^2(4)=330.39, *p*<.001), and Reward Reliability (χ^2(6)=21.98, *p*=.001). Interactions between Reward Reliability and Effort Level (χ^2(2)=18.63, *p*<.001) and Reward Reliability and Reward Level (χ^2(2)=6.02, *p*=.05) were also significant.

In general participants were found to prefer Low Effort trials over High Effort trials (β=1.85, *SE*=.15, *z*=12.11, *p*<.001). Participants were also found to choose High Reward trials much more often than Low Reward trials (β=3.26, *SE*=.16, *z*=20.51, *p*<.001).

Post hoc comparisons using Tukey HSD test indicated participants in the Deterministic (β=3.33, *SE*=.27, *z*=12.56, *p*<.001), Probabilistic (β=2.80, *SE*=.25, *z*=11.38, *p*<.001), and Random (β=3.66, *SE*=.28, *z*=13.27, *p*<.001) conditions were significantly more likely to choose the High Reward options compared to Low Reward options. Participants in the Deterministic (β=2.46, *SE*=.26, *z*=9.31, *p*<.001), Probabilistic (β=1.00, *SE*=.24, *z*=4.16, *p*<.001), and Random (β=2.12, *SE*=.27, *z*=7.77, *p*<.001) conditions were also more likely to choose Low Effort trials over High Effort trials. Moreover, participants in the Probabilistic condition were significantly more likely to choose High Effort trials (β=.72, *SE*=.25, *z*=2.90, *p*=.04) and significantly less likely to choose Low Effort (β=-.74, *SE*=.24, *z*=3.07, *p*=.03) compared to participants in the Deterministic condition, but not the Unreliable condition. No significant differences in preferences between participants in the Deterministic and Random conditions were observed.

Participants were also found to be more likely to choose LEHR trials over HEHR (β=1.61, *SE*=.21, *z*=7.84, *p*<.001), LELR (β=3.02, *SE*=.21, *z*=14.40, *p*<.001), and HELR trials (β=5.12, *SE*=.26, *z*=20.00, *p*<.001). Furthermore, participants were found to have a preference for HEHR trials over LELR (β=1.41, *SE*=.18, *z*=7.84, *p*<.001) and HELR trials (β=3.51, *SE*=.22, *z*=15.69, *p*<.001). They were also more likely to choose LELR over HELR trials (β=2.10, *SE*=.22, *z*=9.59, *p*<.001), as indicated by Figure 8.

Physical vs. Mental effort

Comparison of the choices during mental and physical effort trials revealed a significant interaction between Effort Type and Effort Level ($\chi^2(1)=5.44$, *p*=.02). Further analyses revealed, however, no significant differences between mental and physical effort trials across effort levels, as indicated by Figure 8.

Discussion

In general, the results of Experiment 4 suggest that: 1) increasing relative, but not absolute, reward values leads to increased willingness to choose effortful options, 2) reward reliability does affect choices, but only when rewards are probabilistic 3) mental and physical effort are processed in the same way, 4) choices are driven by rewards.

More specifically, in Experiment 4 four hypotheses derived from the V-E-D-M model were investigated: H1, H3, H4, and H5. In line with H1, which suggests that increasing the relative as well as absolute values of rewards available within a task should lead to increased willingness to choose effortful options, participants were found to be more likely to choose high effort trials if they were associated with relatively high rewards. However, contrary to this hypothesis, results of Experiment 4 suggest that increasing the absolute values of rewards did not have the same effect. In general participants were found to make similar choices regardless of whether they experienced Small Rewards or Large Rewards during the task. This result, in turn, suggests that participants utilise the relative, rather than absolute values of rewards when deciding between options.

As far as H3 is concerned, results of Experiment 4 show that reliability of rewards can potentially influence effort based decision-making process, although not in the way suggested by this hypothesis. H3 assumes that increasing reward reliability should lead to increased willingness to choose effortful options. In this experiment participants were found to be more likely to choose high effort trials when rewards were probabilistic compared to when they were deterministic (albeit on mental effort trials only). Therefore, probabilistic rewards were associated with a greater willingness to choose effortful options, contrary to H3.

Furthermore, no significant differences between choices on mental and physical effort trials were observed, in line with H4, which states that processing of these two types of effort should be similar.

Finally, in line with H5, which predicts that if Action Selection is driven by reward values participants should mainly choose trials associated with high rewards, participants in Experiment 4 showed a clear preference for high reward trials, regardless of the amount of effort they were associated with. This suggests that reward values were the most important factor in determining participants' choices.

4.1.5 Experiment 5 (Immediate Execution)

Experiment 5 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Timing of Execution: Immediate Execution vs. Delayed Execution) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on choices associated with either mental or physical effort in two groups of participants: one required to execute their choices immediately after they were made (Immediate Execution group), and one executing their choices after a delay (Delayed Execution group: participants from Experiment 1). Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Selection,

4) H6, which concerns the effects of different types of feedback on choice,

5) H7, which concerns the effects of delaying Action Execution.

Participants' preferences on mental and physical effort trials in Experiment 5 are presented in Figure 9.

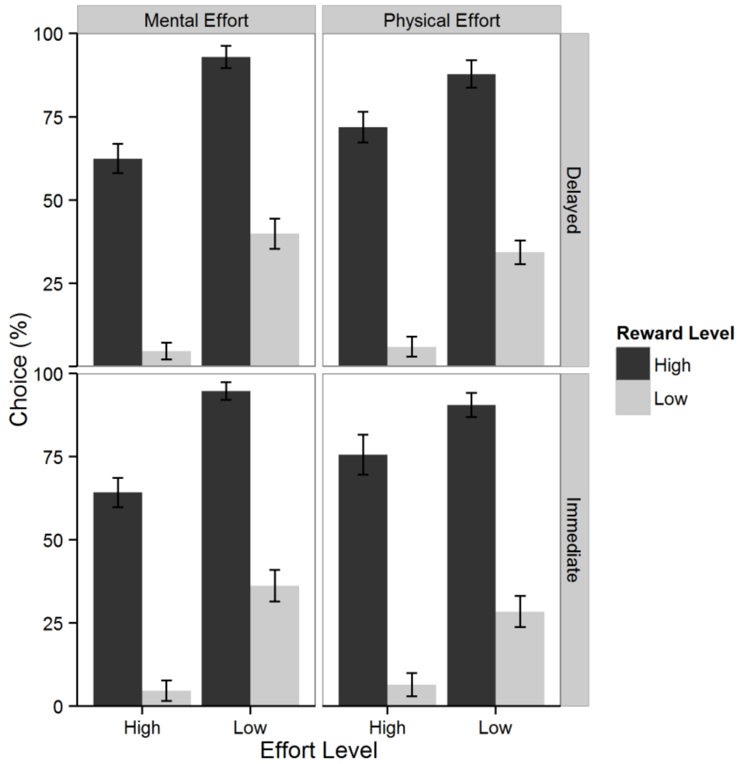


Figure 9. Percentage of times each option was chosen when it was available during mental and physical effort trials in Experiment 5.

Physical effort

Analysis of choices made during physical effort trials in Experiment 2 revealed significant main effects of Effort Level ($\chi^2(2)=170.17$, $p<.001$), Reward Level ($\chi^2(2)=462.22$, $p<.001$), and an interaction between Effort Level and Reward Level ($\chi^2(1)=14.42$, $p<.001$).

In line with the pattern indicated in Figure 9, there was an overall preference for Low Effort over High Effort options ($\beta=1.59$, $SE=.12$, $z=13.13$, $p<.001$), an overall preference for High Reward over Low Reward options ($\beta=3.46$, $SE=.13$, $z=27.12$, $p<.001$), but also an interaction between Effort Level and Reward Level.

Post hoc comparisons using Tukey HSD test showed that participants were more likely to choose LEHR trials over HEHR ($\beta=1.14$, $SE=.16$, $z=7.21$, $p<.001$), LELR ($\beta=3.01$, $SE=.16$, $z=18.85$, $p<.001$), and HELR trials ($\beta=5.04$, $SE=.21$, $z=24.18$, $p<.001$). Furthermore, participants were found to have a preference for HEHR trials over LELR ($\beta=1.87$, $SE=.13$,

z=13.89, p<.001) and HELR trials (β=3.91, *SE*=.19, z=20.78, p<.001). They were also more likely to choose LELR over HELR trials (β=2.04, *SE*=.18, z=11.27, p<.001), as indicated in Figure 9. There was no difference between the choices made when the execution was delayed and when it was immediate.

Mental Effort

Analysis of choices made on mental effort trials revealed significant main effects of Effort Level (χ^2(2)=326.57, p<.001) and Reward Level (χ^2(2)=491.55, p<.001).

In line with the pattern indicated in Figure 9, there was an overall preference for Low Effort over High Effort options (β=2.36, *SE*=.12, z=19.25, p<.001), and an overall preference for High Reward over Low Reward options (β=3.40, *SE*=.13, z=27.12, p<.001).

Post hoc comparisons using Tukey HSD test found that participants were more likely to choose LEHR trials over HEHR (β=1.16, *SE*=.16, z=13.34, p<.001), LELR (β=3.20, *SE*=.16, z=19.49, p<.001), and HELR trials (β=5.76, *SE*=.22, z=25.86, p<.001). Furthermore, participants were found to have a preference for HEHR trials over LELR (β=1.04, *SE*=.11, z=9.53, p<.001) and HELR trials (β=3.59, *SE*=.18, z=19.61, p<.001). They were also more likely to choose LELR over HELR trials (β=2.56, *SE*=.18, z=14.08, p<.001), as demonstrated in Figure 9. There was no difference between the choices made when the execution was delayed and when it was immediate.

Physical vs. Mental effort

Comparison of the choices made on mental and physical effort trials revealed a significant main effect Effort Type (χ^2(2)=30.52, p<.001), as well as a significant interaction between Effort Type and Effort Level (χ^2(1)=30.52, p<.001).

Further analyses using Tukey HSD revealed that participants were less likely to choose High Effort trials (β=-.44, *SE*=.11, z=-4.14, p<.001) and more likely to choose Low Effort trials (β=.38, *SE*=.10, z=3.76, p=.001) on mental effort trials compared to physical effort trials, as indicated by Figure 9.

Discussion

In general, the results of Experiment 5 suggest that: 1) increased relative reward values lead to increased willingness to choose effortful options, 2) mental and physical effort are processed differently during Action Selection, 3) choices are driven by rewards, 4), feedback does not influence the choices people make, and 5) delayed execution does not affect the choices people make.

More specifically, in Experiment 5 five hypotheses derived from the V-E-D-M model were investigated: H1, H4, H5, H6, and H7. In line with the results of the previous studies described in this chapter, the findings from this experiment supported H1, which suggests that increasing reward values leads to increased willingness to choose effortful actions, as participants were found to be more likely to choose high effort trials if they were associated with high rewards.

Contrary to H4, which declares that mental and physical effort should be processed in a similar way, differences between choices regarding mental and physical effort were observed in this experiment. Participants showed a greater preference for low effort trials when mental effort was involved. Nevertheless, it is hard to determine precisely what the basis for this difference is. Alternative explanations are considered in more detail in the general discussion in Chapter 7.

As far as H5 is concerned, results of Experiment 5 supported the claim that during Action Selection choices are driven by reward values. Participants were found to have the strongest preference for the options associated with high rewards, regardless of the amount of effort required to obtain them.

Type of feedback present during the task was shown not to have any effect on the choices people made during this experiment, contrary to H6, which predicts that different types of outcome feedback should affect Action Selection differently.

Furthermore, no differences were found between choices of participants who experienced immediate and delayed Action Execution, contrary to H7, which states that delaying Action Execution should lead to increased willingness to choose effortful actions.

4.1.6 Experiment 6 (PD study)

Experiment 6 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Group: PD vs. HC) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on choices associated with either mental or physical effort in PD patients and HCs.

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Selection,

4) H8, which concerns the effects of altered dopaminergic transmission on choice.

Participants' preferences on mental and physical effort trials are presented in Figure 10.

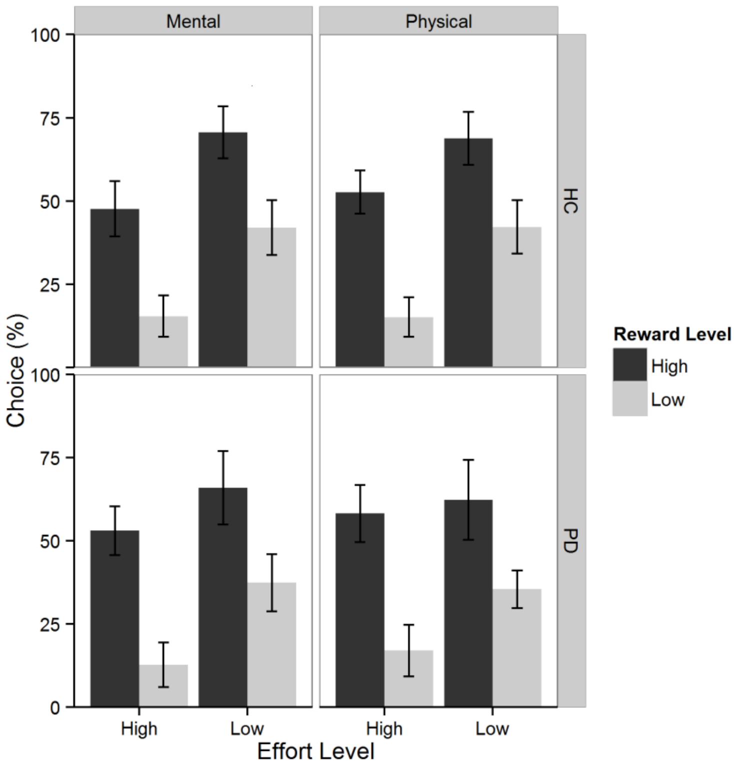


Figure 10. Percentage of times each option was chosen when it was available on mental and physical effort trials in Experiment 6.

Physical effort

Analysis of choices participants made on physical effort trials revealed significant main effects of Effort Level ($\chi^2(3)=46.59$, $p<.001$,) and Reward Level ($\chi^2(2)=105.16$, $p<.001$). Interactions between Effort Level and Reward Level ($\chi^2(1)=9.60$, p=.001) and between Group and Effort Level ($\chi^2(1)=3.86$, p=.05) were also significant.

In line with the pattern indicated in Figure 10, there was an overall preference for Low Effort over High Effort options (β=.82, *SE*=.13, *z*=6.54, $p<.001$), an overall preference for High Reward over Low Reward options (β=1.52, *SE*=.13, *z*=12.04, $p<.001$).

Post hoc comparisons using Tukey HSD test indicated that participants were more likely to choose LEHR trials over LELR (β=1.12, *SE*=.17, *z*=6.64, $p<.001$) and HELR trials (β=2.33, *SE*=.19, *z*=12.54, $p<.001$), but not HEHR trials ($p=.06$). Furthermore, participants were found to have a preference for HEHR over LELR (β=.70, *SE*=.17, *z*=4.14, $p<.001$) and HELR trials (β=1.91, *SE*=.18, *z*=10.34, $p<.001$). They were also more likely to choose LELR over HELR trials (β=1.21, *SE*=.18, *z*=6.58, $p<.001$), as indicated by Figure 10. No significant differences between PD patients and HCs were observed.

Mental Effort

Analysis of choices made by participants during mental effort trials revealed significant main effects of Effort Level ($\chi^2(2)=60.66$, $p<.001$) and Reward Level ($\chi^2(2)=99.89$, $p<.001$). Interaction between Effort Level and Reward Level was also significant ($\chi^2(1)=6.33$, $p=.01$).

In line with the pattern indicated in Figure 10, there was an overall preference for Low Effort over High Effort options (β=1.07, *SE*=.13, *z*=8.28, $p<.001$), and an overall preference for High Reward over Low Reward options (β=1.48, *SE*=.13, *z*=11.32, $p<.001$).

Post hoc comparisons using Tukey HSD test indicated that participants were more likely to choose LEHR trials over HEHR (β=.75, *SE*=.17, *z*=4.39, $p<.001$), LELR (β=1.16, *SE*=.17, *z*=6.66, $p<.001$), and HELR trials (β=2.56, *SE*=.20, *z*=12.90, $p<.001$). Furthermore, participants were found to have a preference for HEHR trials over HELR trials (β=1.81, *SE*=.19, *z*=9.52, $p<.001$), but not LELR trials ($p=.06$). They were also more likely to choose LELR over HELR (β=1.40, *SE*=.19, *z*=7.33, $p<.001$) trials, as indicated by Figure 10.

Physical vs. Mental effort

Additional analysis comparing choices of participants on mental and physical effort trials revealed no effect of Effort Type, indicating that there were no significant differences between choices made on mental and physical effort trials, in line with Figure 10.

Discussion

In general, the results of Experiment 6 suggest that: 1) increased relative reward values lead to increased willingness to choose effortful options, 2) mental and physical effort are processed in a similar way during Action Selection, 3) choices are driven by rewards, 4), dopamine might not be crucial for overcoming effort costs during Action Selection.

More specifically, in Experiment 6 four hypotheses derived from the V-E-D-M model were investigated: H1, H4, H5, and H8. In line with the results of the previous studies described in this chapter, results of Experiment 6 supported H1, which states that increasing relative reward values should lead to increased willingness to choose effortful trials. Both PD patients and HCs were found to be more likely to choose high effort trials when they were associated with high rewards. Results of this experiment also supported H4, which predicts that mental and physical effort should be processed in a similar way, as no differences between choices made on mental and physical effort trials were found.

Furthermore, results of Experiment 6 suggested that Action Selection during effort-based decision-making tasks is driven primarily by reward values, and not effort requirements (H5), as participants in Experiment 6 were found to have a strong preference for high reward options regardless of the amount of effort associated with them.

In line with a large number of studies indicating an important role of dopamine for effort-based decision-making, it has been assumed that decreased dopaminergic transmission associated with PD should lead to decreased willingness to choose effortful options in PD patients (H8). However, no differences between PD patients and HCs were observed in Experiment 6, suggesting that dopamine might not be crucial during Action Selection stage of effort-based decision-making.

4.2 General Discussion

The V-E-D-M model makes specific assumptions about how effort and rewards affect effort-based decision-making. For example, it assumes that manipulating reward magnitude/valence/reliability, or the type of effort required has the potential to affect behaviour during Action Selection and Action Execution stages of decision-making. It also asserts that changing the type of feedback available or delaying the presentation of feedback impacts decision-making behaviours. One of the methods of establishing the validity of these assumptions is investigating the choices people make during effort-based decision-making process. Such investigations were the focus of the six experiments described in this chapter, providing an important insight into the effects of different manipulations on choices made during effort-based decision-making. Six areas of interest derived from the V-E-D-M model were investigated in these experiments: 1) Reward manipulations, 2) Effort manipulations, 3) Importance of effort/reward during Action Selection and Action Execution, 4) Outcome feedback, 5) Delayed Action Execution, 6) Neural underpinnings.

The rest of this chapter will survey the general pattern of findings across the six experiments with respect to the six areas of interest listed above, describing the implications of these findings for the assumptions of the V-E-D-M model.

1) Reward manipulations

a) Effects of manipulating reward magnitude on choice

One of the implicit assumptions of the V-E-D-M model is that increasing reward magnitude should lead to increased willingness to choose effortful actions associated with higher rewards. This assumption was supported in all six experiments. However, this increased willingness to exert effort for rewards seemed to depend on the relative difference between rewards available within the task, rather than absolute monetary values of rewards. These findings suggest that, as far as the choice behaviour is concerned, increasing the relative, but not absolute, value of rewards leads to increased willingness to choose effortful options.

b) Effects of manipulating reward valence on choice

Another assumption which the V-E-D-M model makes is that manipulating reward valence should affect the choices people make during an effort-based decision-making task, reducing people's willingness to choose effortful options in the face of losses. This assumption has largely been confirmed by the results of Experiment 2, which found that participants in the Loss group were more likely to choose low effort trials compared to participants in the Gain group.

c) Effects of manipulating reward reliability on choice

In addition to reward magnitude and valence, reward reliability is also supposed to have an impact on the choices people make, according to the V-E-D-M model. More specifically, the model assumes that willingness to exert effort should increase with reward reliability. This claim was investigated in Experiments 3 and 4. In general, the findings of these experiments do not support this hypothesis. They suggest that when rewards are deterministic or random, participants concentrate more on the amount of effort that is required to obtain them. When the rewards are probabilistic, however, participants seem to be less concerned with the effort requirements. This is possibly because, having limited experience with the task, participants assume that the probability of obtaining a reward might be associated with the amount of effort put in during the task, and so are more willing to choose high effort options to maximize the rewards obtained.

2) Effort manipulations

The V-E-D-M model assumes that manipulating the type of effort (mental or physical) that is required during a task should not have a big impact on the choices people make, as mental and physical effort are processed in a similar manner throughout the stages of effort-based decision-making. This assumption was investigated in the six experiments described above. The findings of these experiments were inconclusive. Therefore, the question of whether mental and physical effort are processed in a similar way during effort-based decision-making requires further investigations.

3) Importance of effort/reward during Action Selection and Action Execution

Another question regarding the influence of reward and effort on effort-based decision-making is: which one of these two factors is more important when making choices between options? This issue was investigated in all of the experiments described in this chapter. In these experiments reward has been found to be the most important factor driving Action Selection, determining the choices participants made regardless of the circumstances. These results suggest that when people need to decide between options that require exerting effort for monetary rewards, the factor that will influence their choices the most is the reward value.

4) Outcome feedback

Another assumption that V-E-D-M model makes is that manipulating the type of feedback available at the end of each trial should have an effect on the effort-based decision-making process. This assumption has not been supported by the results of Experiments 1 and 5, which included feedback manipulations, as no effect of feedback was found in these experiments. Therefore, it seems that changing the amount of outcome information about rewards does not influence the choices people make, contrary to what has been assumed by the V-E-D-M model.

5) Delayed Action Execution

According to the V-E-D-M model, experiencing the outcome of the decision-making process serves as a basis for updating representations on which future choices are based. Preventing the experience of an outcome after a choice is made should prevent learning, potentially influencing future choices. This assumption has been tested in Experiment 5, in which the choices of participants experiencing immediate or delayed Action Execution were compared. No differences between the two groups were found. Such result suggests that learning might not influence decision-making as strongly as assumed by the V-E-D-M model, at least within the limited learning experience available in this particular task.

6) Neural underpinnings

The V-E-D-M model assumes that neurotransmitter dopamine plays an important role during all stages of effort-based decision-making. Direct implication of this assumption is that in PD patients, in whom dopamine levels in the brain are depleted, all stages of decision-making should be affected. This assumption was tested in Experiment 6. No differences between choices made by PD patients and HCs were found, suggesting that dopamine might not be as important when making choices regarding effort as previously thought. It has to be noted, however, that PD patients in this particular experiment were tested on dopaminergic medication, which could potentially affect the results.

4.3 Summary

For the most part, results of the studies presented above support the key hypotheses of the V-E-D-M model (for example regarding the effects of increasing relative reward values, changing reward valence, or manipulating effort type) which is encouraging. They also help to clarify certain assumptions of the model. However, these investigations do not provide the full picture, as they do not inform about the effects of manipulating reward, effort and feedback characteristics on effort exertion during Action Execution. Therefore, in the next two chapters the effects of changing reward magnitude, valence, and reliability, as well as the effort type and feedback on effort exertion during Action Execution will be examined, to provide further information regarding the assumptions of the V-E-D-M model.

CHAPTER 5: Experimental Studies - Effort Exertion

According to the V-E-D-M model of effort-based decision-making, manipulating different aspects of reward and effort should potentially affect both the choices people make and the amount of effort they exert during a task. Examining people's choices during a novel effort-based decision-making task, as described in Chapter 4, provides partial support for this assumption. However, to get the full picture of how changing aspects of effort and reward affects decision-making, effort exertion during the task execution stage needs to be examined as well. Therefore, in this chapter the effects of manipulating reward, effort, and feedback on the amount of effort participants put in in a newly developed effort-based decision-making task were investigated. The specific areas covered by these investigations were: 1) **Reward manipulations,** 2) **Effort manipulations,** 3) **Importance of effort/reward during Action Selection and Action Execution,** 4) **Outcome feedback,** 5) **Delayed Action Execution,** 6) **Neural underpinnings.**

As far as **Reward manipulations** are concerned, in this chapter the effects of a) increasing relative as well as absolute reward values, b) changing reward valence (from gain to loss), and c) changing reward reliability on participants' grip strength (physical effort) and response times (mental effort) were examined. Furthermore, participants' performance on mental and physical effort trials was compared, to investigate the effects of **Effort manipulations**. **Importance of effort/reward during Action Execution** was also examined through investigating participants' effort exertion on trials associated with different levels of effort and reward. The effects of different types of **Outcome feedback,** as well as the effects of **Delaying Action Execution** on the amount of effort participants put in were explored as well. Finally, the role of dopamine during Action Execution stage is investigated, in an effort to explore the **Neural underpinnings** of effort-based decision-making.

These topics were investigated in six studies which used the novel effort-based decision-making task described in Chapter 3. The task consisted of three phases: Training phase, Choice phase, and Execution phase. This chapter focuses specifically on participants' performance during the Execution phase. During this phase participants were asked to squeeze the hand grip device (physical effort) or to solve simple mathematical equations (mental effort) to obtain small monetary rewards (see Figure 11). The amount of effort and reward on each trial depended on the choices participants made during the Choice phase. On the physical effort trials effort exertion was measured through recording the grip strength of participants, with stronger grips signifying higher effort exertion. On the mental effort trials participants' response times were examined. Slower response times were assumed to be associated with higher effort exertion. Participants' performance was analysed using LMMs (physical effort) and GLMMs assuming gamma or inverse distributions (mental effort). The results of these analyses are presented in this chapter.

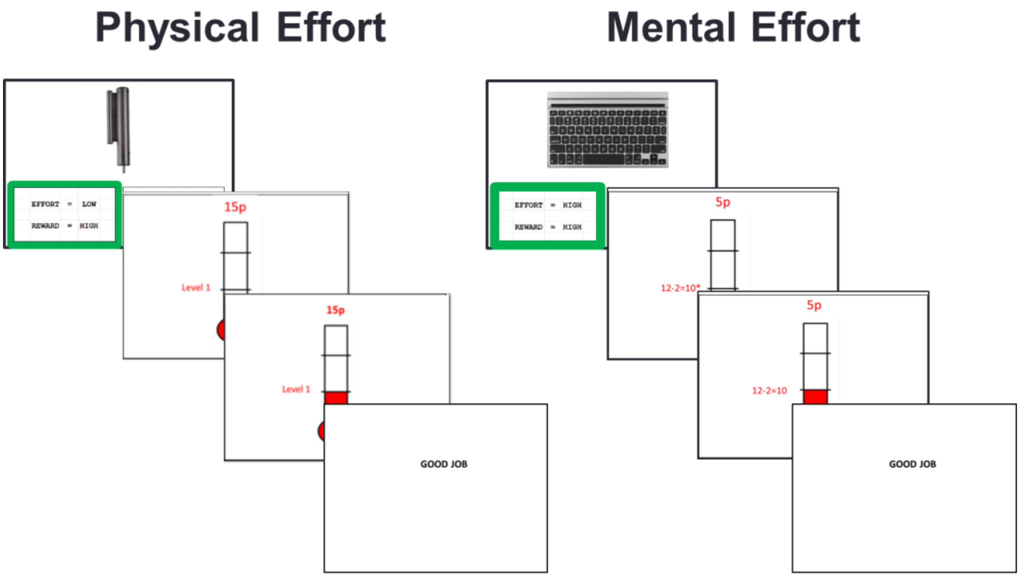


Figure 11. Example of trials participants had to complete during the Execution phase

The specific hypotheses investigated were:

H1: Increasing incentives available in a task should increase the amount of effort people exert through increasing the grip strength on physical effort trials and prolonging response times on mental effort trials. This increase should be observed for both the relative and absolute reward values.

H2: Participants in the Loss group should exert more effort than participants in the Gain group, to avoid losing money.

H3: Positive relationship between the probability of obtaining rewards and the amount of effort exerted should be observed.

H4: Even though direct comparison of mental and physical effort during the Action Execution stage is not possible due to the use of different measures to examine these two types of effort, the pattern of results observed for mental and physical effort should be similar.

H5: If behaviour during Action Execution is driven by reward values, effort exerted by participants should be proportional to the reward value available during each trial. If, however, it is driven by effort requirements, effort exertion should be proportional to the effort level required.

H6: Type of feedback present during a task should have an effect on the amount of effort people exert during a task, with participants exerting the most effort on cumulative feedback trials, followed by discreet and simple feedback trials.

H7: Participants experiencing the outcome of their decisions immediately should invest different amount of effort compared to participants who experience the outcome after a delay.

H8: Depletion of dopamine levels in PD should lead to reduced effort exertion (reduced grip strength and shortened response times) on mental and physical effort trials.

In Chapter 5 the results of studies designed to investigate these hypotheses are examined and their implications are discussed in the context of the assumptions of the V-E-D-M model.

Summary of the findings of different experiments is presented in Table 6.

Table 5. Results of the analyses of choices made by participants during six main experiments with regard to the 8 hypotheses investigated. "+" represents hypothesis supported by the results of the experiment, "-" represents hypothesis for which support was not found, "partial" represents hypothesis for which partial support was found. In column H5, the factor which was found to drive behaviour during choice is specified.

Experiment	Hypotheses							
	H1 Effects of manipulating reward magnitude	H2 Effects of manipulating reward valence	H3 Effects of manipulating reward reliability	H4 Comparison of mental/physical effort	H5 Reward/Effort driving behaviour	H6 Effects of manipulating reward feedback	H7 Effects of immediate/delayed execution	H8 Effects of dopamine depletion
Experiment 1 (Gains)	+			-	reward	-		
Experiment 2 (Losses)	+	+		+	reward			
Experiment 3 (Reliability)	+		partial	+	reward			
Experiment 4 (Increased Incentives)	relative: + absolute -		partial	+	reward			
Experiment 5 (Immediate Execution)	+			-	reward	-	-	
Experiment 6 (PD study)	+			+	reward			-

5.1 Results

In each of the following sections experimental design is described first, followed by the results from the physical effort trials, mental effort trials, and the comparison of the two types of trials. At the end of each section the findings are discussed in the context of the experimental hypotheses.

Performance of participants on different types of trials (HEHR, HELR, LEHR, LELR) is presented separately for mental and physical effort in Appendix B.

5.1.1 Experiment 1 (Gains)

Experiment 1 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on grip strength (physical effort) and response times (mental effort). Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

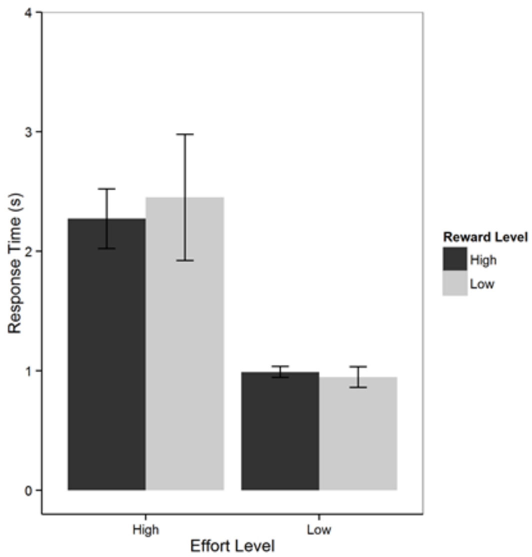
1) H1, which concerns the associations between relative reward values and effort,

2) H4, which concerns the differences between mental and physical effort,

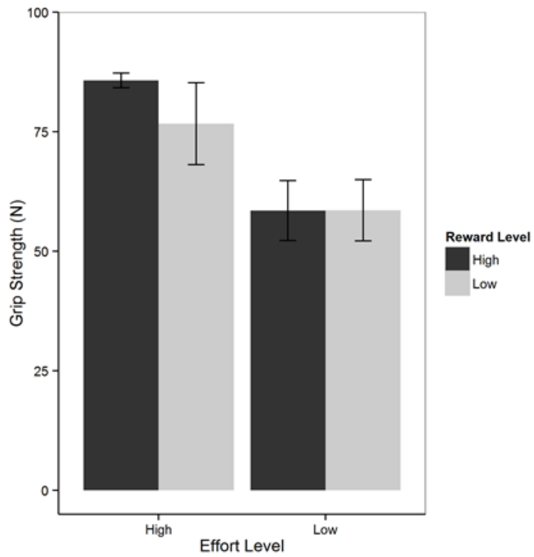
3) H5, which concerns the factors (reward/effort) driving Action Execution,

4) H6, which concerns the effects of different types of feedback on effort exertion.

Participants' performance on physical and mental effort trials is presented in Figure 12.



a) Response times on mental effort trials



b) Grip strength on physical effort trials

Figure 12. Performance on mental (a) and physical (b) effort trials in Experiment 1.

P*hysical Effort*

Analysis of the grip strength during physical effort trials revealed a significant main effect of Effort Level (χ^2(1)=98.12, *p*<.001), as participants were found to squeeze less hard when the effort was low (β=47.77, *SE*=3.65, *t*(99.33)=13.08, *p*<.001).

Mental Effort

Analysis of response times during mental effort trials revealed a significant main effect of Effort Level (χ^2(1)=193.61, *p*<.001), as participants were found to be slower on High Effort trials (β=-.58, *SE*=.03, *z*=-20.06, *p*<.001).

Physical vs. Mental Effort

The pattern of results during the execution of mental and physical effort was found to be similar, with participants found to exert less effort on Low Effort trials regardless of the type of effort required, as indicated by Figure 12.

Discussion

In general, the results of Experiment 1 suggest that: 1) increased reward values do not translate into increased effort exertion, 2) mental and physical effort are processed in a similar way during Action Execution, 3) effort exertion is driven by effort requirements, and 4) feedback does not have a strong influence on effort exertion.

More specifically, Experiment 1 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H4, H5 and H6. According to H1, increasing the incentive value should increase the amount of effort people exert, increasing the grip strength on physical effort trials and prolonging response times on mental effort trials. However, no such increase in effort exertion in response to high rewards was observed in Experiment 1. This suggests that reward values might not have as strong influence on effort exertion as assumed by the V-E-D-M model. The same pattern of results was observed on mental and physical effort trials, suggesting that these two types of effort are processed in a similar way during effort exertion, in line with H4.

Furthermore, according to H5, if behaviour during Action Execution is driven by reward values, effort exerted by participants in Experiment 1 should be proportional to the reward value available during each trial. However, no such effect was observed in this experiment. Instead, the results of Experiment 1 point to the dominant role of effort requirements in determining effort exertion, as participants were found to exert more effort on high effort trials, regardless of the amount of reward associated with them.

Contrary to H6, which predicts that different types of feedback should affect effort exertion differently, the type of feedback present during the task was found not to have any effect on the effort exerted during the task. This suggests that the effects of feedback on effort-based decision-making might be less pronounced than assumed by the V-E-D-M model.

5.1.2 Experiment 2 (Losses)

Experiment 2 was a 2 (Effort Level: High vs. Low) x 2 (Stakes Level: High vs. Low) x 2 (Effort Type: Mental vs Physical) x 2 (Reward Valence: Gain vs. Loss) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low stakes on grip strength (physical effort trials) and response times (mental effort trials) in two groups of participants: one trying to win monetary rewards (Gain group: participants from Experiment 1) and one trying to avoid losing them (Loss group). In contrast to Experiment 1, where options associated with high and low rewards were compared, in this experiment the influence of option stake was investigated. In the Gain group High Stake (HS) trials were associated with an opportunity to win 15p and Low Stakes (LS) trials with an opportunity to win 5p. In the Loss group HS trials were associated with potential loss of 15p, whereas LS trials were associated with potential loss of 5p. Participants were randomly assigned to one of the three Reward

Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H2, which concerns the effects of gains and losses,

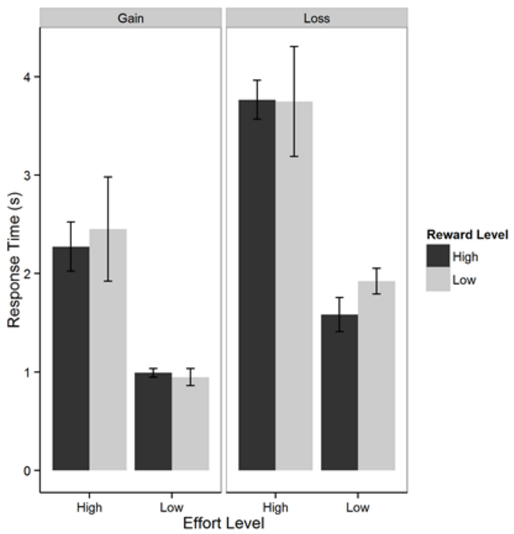
3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Execution,

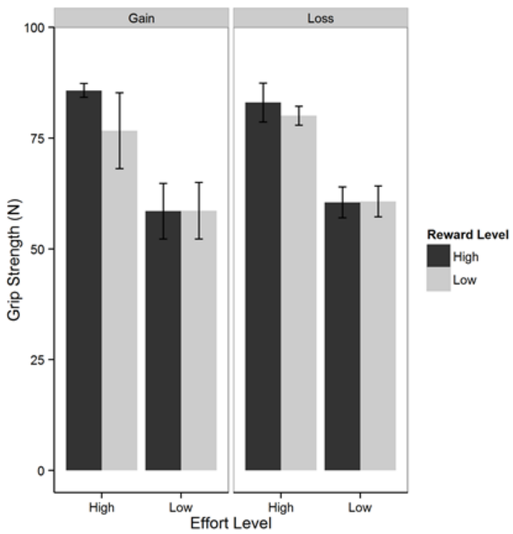
5) H6, which concerns the effects of different types of feedback on effort exertion.

Since participants in the Cumulative feedback condition did not choose the options associated with high effort and a potential loss of 15p at all, feedback had to be removed from the analyses, as otherwise the model would not converge due to zero cell counts for categorical predictors.

Participants' performance on physical and mental effort trials in Experiment 2 is presented in Figure 13.



a) Response times on mental effort trials



b) Grip strength on physical effort trials

Figure 13. Performance on mental (a) and physical (b) effort trials in Experiment 2.

Physical Effort

Analysis of grip strength during physical effort trials revealed significant main effects of Effort Level ($\chi^2(2)=234.44$, $p<.001$) and Stakes Level ($\chi^2(2)=14.43$, $p<.001$). Interaction between Effort Level and Stakes Level was also significant ($\chi^2(1)=9.96$, $p=.002$).

In general, participants were found to squeeze harder on High Effort trials compared to Low Effort trials ($\beta=-43.38$, $SE=2.08$, $t(203.71)=-20.89$, $p=.001$), and to squeeze harder on the High Stakes trials compared to Low Stakes trials ($\beta=-6.34$, $SE=2.15$, $t(214.44)=-2.95$, $p=.004$).

Post hoc comparisons using Tukey HSD test indicated that participants squeezed harder on High Stakes compared to Low Stakes trials when effort was high ($\beta=-13.14$, $SE=3.44$, $t(222.03)=-3.82$, $p=.001$), but not low ($p=.99$). Participants also squeezed harder on High Effort trials compared to Low Effort trials when the stakes were high ($\beta=-50.18$, $SE=3.06$, $t(210.43)=-16.37$, $p<.001$) and when they were low ($\beta=-36.58$, $SE=2.91$, $t(207.93)=-12.58$, $p<.001$).

Mental Effort

Analysis of response times during mental effort trials revealed main effects of Effort Level ($\chi^2(3)=369.41$, $p<.001$), Stakes Level ($\chi^2(3)=22.30$, $p<.001$) and Reward Valence ($\chi^2(3)=57.40$, $p<.001$). Interactions between Effort Level and Stakes Level ($\chi^2(1)=6.66$, $p=.01$) and Reward Valence and Stakes Level ($\chi^2(1)=3.96$, $p=.05$) were also significant.

In general, participants were found to respond slower on High Effort trials compared to Low Effort trials ($\beta=0.84$, $SE=.03$, $z=28.35$, $p=.001$), but to be equally fast on the High Stakes trials compared to Low Stakes trials ($p=.09$).

Post hoc comparisons using Tukey HSD test indicated that participants were significantly slower on High Effort trials compared to Low Effort trials regardless of whether the stakes were high ($\beta=.75$, $SE=.05$, $z=16.16$, $p<.001$) or low ($\beta=.92$, $SE=.04$, $z=21.28$, $p<.001$). Participants were also found to be slower on High Stakes trials compared to Low Stakes trials when the effort required was low ($\beta=.15$, $SE=.03$, $z=4.27$, $p<.001$), but not high ($p=.96$). In addition, participants were found to be significantly slower in the Losses experiment, regardless of whether the stakes were high ($\beta=.60$, $SE=.07$, $z=8.74$, $p<.001$) or low ($\beta=.48$, $SE=.07$, $z=7.19$, $p<.001$).

Physical vs. Mental effort

Participants were found to react differently to High Stakes trials when different types of effort were required, investing more effort on High Stakes than Low Stakes trials when effort was high on physical effort trials, but investing more effort on High Stakes compared to Low Stakes trials when effort was low on mental effort trials. Secondly, mental effort was found to be somewhat more sensitive to the valence manipulation than physical effort, as participants were found to put in more effort when they were facing losses, rather than wins on mental effort trials. No such effect was observed on the physical effort trials. Therefore, inspection of the pattern of effort exertion during physical and mental effort trials in Experiment 2 indicates that these two types of effort might be processed differently during effort exertion.

Discussion

In general, the results of Experiment 2 suggest that: 1) increasing the monetary stakes can lead to increased effort exertion, 2) when losses are a possibility, effort exertion can increase, but only on mental effort trials 3) mental and physical effort seem to be processed in different ways, 4) effort exertion is driven primarily by effort requirements.

More specifically, Experiment 2 was set up to investigate five hypotheses derived from the V-E-D-M model: H1, H2, H4, H5, and H6. As far as H1 is concerned, which assumes that increasing the amount of money at stake should lead to increased effort exertion, the results of this experiment were mixed. On the physical effort trials increasing the stakes led to increased effort exertion when effort required was high, but not low. On the mental effort trials, on the other hand, participants were found to put in more effort for high stakes when effort required was low, but not high. Possible explanations for such pattern of results will be discussed in the general discussion in Chapter 7.

Furthermore, participants facing potential losses were found to put in more mental effort than participants facing potential gains. This result suggests that participants in the Loss group were more risk averse than participants in the Gain group, in line with H2, which states that participants in the Loss group should exert more effort to reduce the risk of failure. Nevertheless, this effect was limited to mental effort trials, which suggest that people experiencing losses might not be risk averse in all circumstances.

Differences in the pattern of performance on the mental and physical effort trials observed in Experiment 2 suggest that mental and physical effort might be processed differently during the Action Execution, contrary to H4, which states that these two types of effort should be processed in a similar way. Further consideration of this can be found in Chapter 7.

As far as the role of reward level and effort requirements in driving effort exertion during Action Execution is concerned (H5), the results seem to suggest that effort requirements are the one consistent factor determining the amount of effort put in during the trials in different task set ups. Nevertheless, monetary outcomes also seem to play a role to some extent, as participants were found to increase their effort expenditure on high stakes trials in certain circumstances (e.g. on low mental effort trials and high physical effort trials).

5.1.3 Experiment 3 (Reliability)

Experiment 3 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 3 (Reward Reliability: Deterministic vs. Probabilistic vs. Unreliable) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on grip strength (physical effort) and response times (mental effort) in three groups: Deterministic (reward present on 100% of successful trials), Probabilistic (reward present on 75% of successful trials and 25% of unsuccessful trials), or Unreliable (reward present on 50% of the trials, regardless of whether they were successful or not).

These manipulations served to address the following hypotheses:

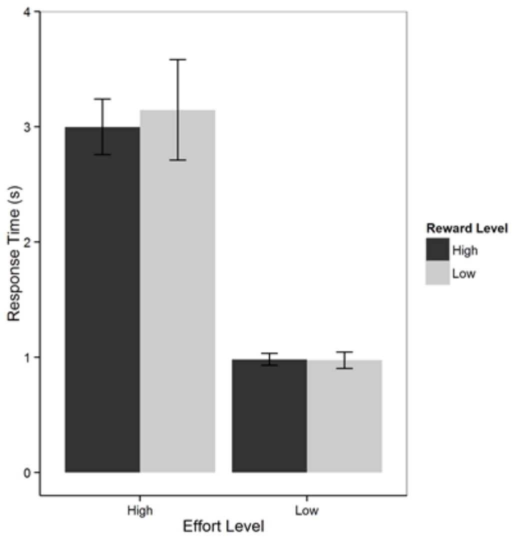
1) H1, which concerns the associations between relative reward values and effort,

2) H3, which concerns the effects of reward reliability

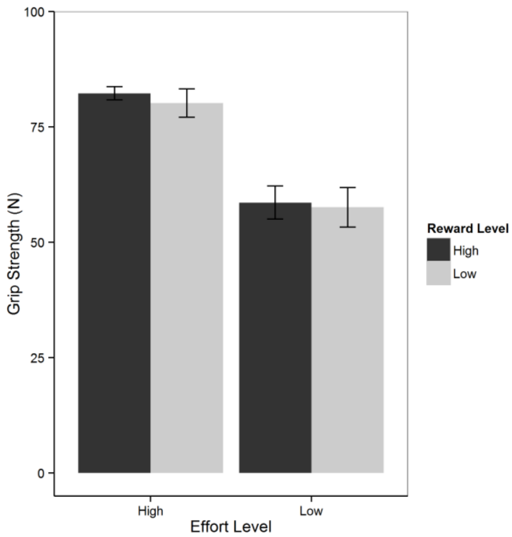
3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Execution.

Participants' performance on physical and mental effort trials in Experiment 3 is presented in Figure 14.



a) Response times on mental effort trials



b) Grip strength on physical effort trials

Figure 14. Performance on mental (a) and physical (b) effort trials in Experiment 3.

Physical Effort

Analysis of grip strength during physical effort trials revealed a significant main effect of Effort Level ($\chi^2(1)=190.86$, $p<.001$). Participants were found to squeeze harder on High Effort trials compared to Low Effort trials ($\beta=-54.24$, $SE=2.34$, $t(106.85)=-23.22$, $p<.001$).

Mental Effort

Analysis of response times during mental effort trials revealed a significant main effect of Effort Level ($\chi^2(1)=287.18$, $p<.001$). Participants were found to respond significantly slower on High Effort trials compared to Low Effort trials ($\beta=-.68$, $SE=.02$, $z=-28.56$, $p<.001$).

Physical vs. Mental Effort

The pattern of results during the execution of mental and physical effort was found to be similar, with participants exerting less effort on Low Effort trials regardless of the type of effort required, as indicated by Figure 14.

Discussion

In general, the results of Experiment 3 suggest that: 1) increasing the monetary rewards does not influence effort exertion 2) reward reliability does not influence effort exertion 3) mental and physical effort seem to be processed in a similar way during Action Execution, 4) effort exertion is driven primarily by effort requirements.

More specifically, Experiment 3 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H3, H4, and H5. Contrary to H1, which states that higher reward values should be associated with increased effort expenditure, no effects of increasing incentive value on effort exertion were found in this experiment. Furthermore, no relationship between the reward reliability and effort exertion was observed, contrary to H3, which asserts that effort expenditure should increase in line with reward reliability. The same pattern of results was obtained on mental and physical effort trials, in line with H4, which predicts that these two types of effort should be processed in the same way during Action Execution. Furthermore, the fact that the level of effort was the only determinant of the amount of effort exerted during this experiment seems to suggest that effort requirements, rather than reward values drive effort exertion during Action Execution (H5).

5.1.4 Experiment 4 (Increased Incentives)

Experiment 4 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Reward Magnitude: Large Rewards vs. Small Rewards) x 3 (Reward Reliability: Deterministic vs. Probabilistic vs. Unreliable) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on grip strength (physical effort) and response times (mental effort) in two groups: one exerting effort for small rewards (15p and 5p) (Small Rewards group: participants from Experiment 1) and one exerting effort for large rewards (30p and 15p) (Large Rewards group). Participants were randomly assigned to one of the three groups: Deterministic (reward present on 100% of successful trials), Probabilistic (reward present on 75% of successful trials and 25% of unsuccessful trials), or Unreliable (reward present on 50% of the trials, regardless of whether they were successful or not).

These manipulations served to address the following hypotheses:

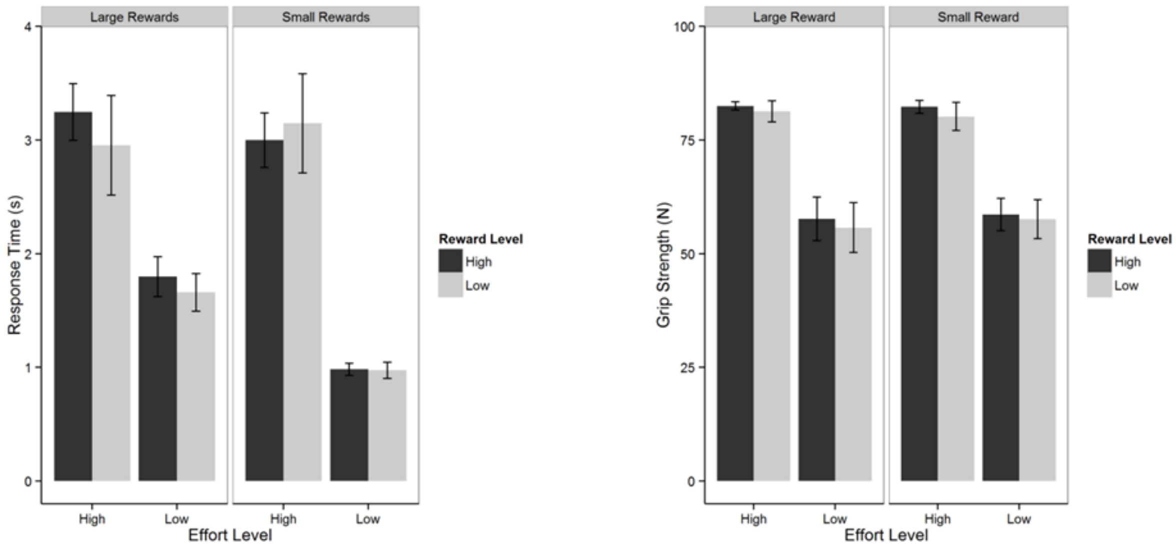
1) H1, which concerns the associations between relative as well as absolute reward values and effort,

2) H3, which concerns the effects of reward reliability,

3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Execution.

Participants' performance on physical and mental effort trials in Experiment 4 is presented in Figure 15.



a) Response times on mental effort trials *b)* Grip strength on physical effort trials

Figure 15. Performance on physical (a) and mental (b) effort trials in Experiment 4

Physical Effort

Analysis of grip strength during physical effort trials revealed a significant main effect of Effort Level ($\chi^2(2)$=338.63, p<.001), as participants were found to squeeze harder when effort required was high (β=-54.30, SE=1.73, t(183.6)=-31.43, p<.001).

Mental Effort

Analysis of response times during the mental effort trials revealed significant main effects of Effort Level ($\chi^2(3)$=428.63, p<.001) and Reward Magnitude ($\chi^2(3)$=99.89, p<.001). Interaction between Reward Magnitude and Effort Level was also found to be significant ($\chi^2(1)$=76.78, p<.001).

In general, participants were found to respond slower on High Effort trials compared to Low Effort trials (β=.86, SE=.03, z=30.91, p<.001). Furthermore, participants experiencing Large Rewards were found to respond slower than participants experiencing Small Rewards (β=.29, SE=.06, z=4.86, p<.001)

Post hoc comparisons using Tukey HSD test indicated that participants in the group experiencing Large Rewards were slower on Low Effort trials than participants from the group experiencing Small Rewards (β=.55, *SE*=.06, *z*=8.62, *p*<.001). No such effect was observed on High Effort trials (*p*=.82). Participants were also significantly slower on High Effort trials compared to Low Effort trials in the Large Rewards (β=.62, *SE*=.04, *z*=15.30, *p*<.001) and Small Rewards groups (β=1.11, *SE*=.04, *z*=31.42, *p*<.001).

Physical vs. Mental Effort

The pattern of results observed during physical and mental effort trials seems to suggest that mental effort exertion is more sensitive to the absolute reward values than physical effort exertion, as participants in the Large Rewards group were found to put in more effort on Low Effort trials than participants in the Small Rewards group when mental effort was required. No such effect was observed on physical effort trials. Therefore, inspection of the pattern of performance during physical and mental effort trials suggests that these two types of effort might be processed differently.

Discussion

In general, the results of Experiment 4 suggest that: 1) increasing absolute, but not relative, reward values leads to increased effort expenditure, but only on the low mental effort trials, 2) reward reliability does not affect effort exertion, 3) mental and physical effort seem to be processed differently, 4) effort exertion is driven by effort requirements.

More specifically, Experiment 4 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H3, H4, and H5. Contrary to H1, which predicts that participants should exert more effort on trials associated with higher relative, as well as absolute, rewards, the results of this experiment suggest that increasing relative reward values does not increase effort expenditure during Action Execution. Nevertheless, mental effort exertion seems to depend to some extent on the absolute reward values, as participants in the Large Rewards group were found to exert more effort on low mental effort trials than participants in the Small Rewards group. No effect of reward reliability on effort exertion was observed in this experiment, contrary to H3, which states that effort exertion should increase in line with reward reliability.

The fact that participants were found to respond differently to the absolute reward magnitudes during mental and physical effort trials suggests that mental and physical effort might be processed differently during Action Execution, contrary to H4, which asserts that these two types of effort are processed in a similar way.

Furthermore, the results of Experiment 4 suggest that during Action Execution effort requirements of a task, rather than reward values, drive effort exertion (H5), as participants were found to put in more effort on trials associated with high effort, but not on trials associated with high rewards.

5.1.5 Experiment 5 (Immediate Execution)

Experiment 5 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Timing of Execution: Immediate Execution vs. Delayed Execution) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on grip strength (physical effort) and response times (mental effort) in two groups of participants: one required to execute their choices immediately after they were made (Immediate Execution group), and one executing their choices after a delay (Delayed Execution group: participants from Experiment 1). Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

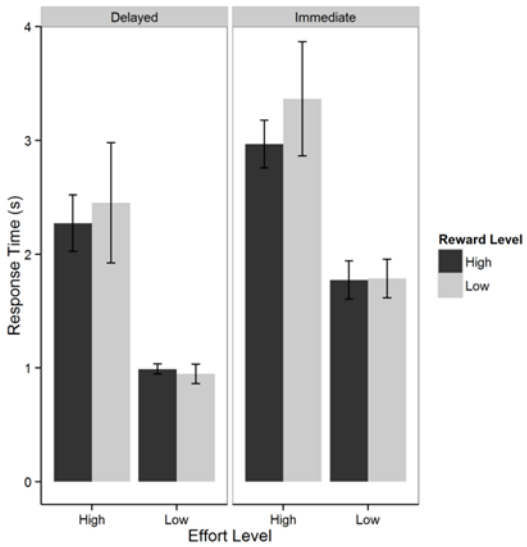
2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Execution,

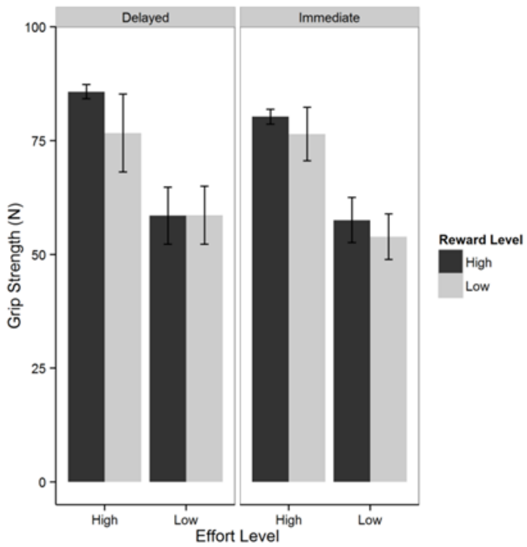
4) H6, which concerns the effects of different types of feedback on effort exertion,

5) H7, which concerns the effects of delaying Action Execution.

Participants' performance on the physical and mental effort trials in Experiment 5 is presented in Figure 16.



a) Response times on mental effort trials



b) Grip strength on physical effort trials

Figure 16. Performance on mental (a) and physical (b) effort trials in Experiment 5.

Physical Effort

Analysis of grip strength during physical effort trials revealed significant main effects of Effort Level (χ^2(3)=190.99, *p*<.001), Reward Level (χ^2(2)=8.17, *p*=.02), and Timing of Execution (χ^2(2)=7.30, *p*=.03).

In general, it was found that participants squeezed harder on High Effort trials compared to Low Effort trials (β=-41.23, *SE*=2.53, *t*(186.74)=-16.30, *p*<.001) and on High Reward trials compared to Low Reward trials (β=-6.80, *SE*=2.53, *t*(185.84)=-2.69, *p*=.007). Participants were also found to squeeze the hand grip device harder when the execution of choice was delayed (β=-10.42, SE=4.71, *t*(74.89)=-2.21, *p*=.03).

Mental Effort

Analysis of response times during mental effort trials revealed main effects of Effort Level (χ^2(3)=317.27, *p*<.001), Timing of Execution (χ^2(2)=64.44, *p*<.001), as well as a significant interaction between Effort Level and Reward Level (χ^2(1)=4.35, *p*=.04) and Timing of Execution and Effort Level (χ^2(2)=29.91, *p*<.001).

In general participants were found to be slower on High Effort trials compared to Low Effort trials (β=.72, *SE*=.03, *z*=23.57, *p*<.001). Participants in the Immediate Execution group were also found to respond slower than participants in the Delayed Execution group (β=.44, *SE*=.06, *z*=6.91, *p*<.001)

Post hoc comparisons using Tukey HSD test indicated that participants in the Immediate Execution group were slower on High Effort trials (β=.29, *SE*=.07, *z*=4.06, *p*<.001) and Low Effort trials (β=.60, *SE*=.07, *z*=8.86, *p*<.001) compared to participants in the Delayed Execution group. Participants were also found to respond slower on High Effort trials compared to Low Effort trials in both Immediate (β=.57, *SE*=.04, *z*=13.56, *p*<.001) and Delayed (β=.88, *SE*=.04, *z*=22.22, *p*<.001) execution groups. No differences in response times to different rewards across effort levels were found.

Physical vs. Mental Effort

Participants were found to put in more effort when execution was delayed on the physical effort trials, and to put in more effort when execution was immediate on the mental effort trials. Furthermore, participants were found to modulate effort exertion in response to different reward values on physical effort trials, but not mental effort trials. Therefore, inspection of the pattern of behaviour observed during the physical and mental effort trials suggests that mental and physical effort might be processed differently during Action Execution.

Discussion

In general, the results of Experiment 5 suggest that: 1) increasing relative reward values leads to increased effort expenditure, but only on physical effort trials 2) mental and physical effort seem to be processed differently, 3) effort exertion is driven by effort requirements, 4) feedback does not influence effort exertion, and 5) delayed execution affects mental and physical effort differently (it increases effort exertion on physical effort trials and decreases on mental effort trials).

More specifically, Experiment 5 was designed to investigate five hypotheses derived from the V-E-D-M model: H1, H4, H5, H6, and H7. As far as H1 is concerned, which states that increasing incentives available in a task should lead to increased effort expenditure, results of Experiment 5 seem to provide partial support for this hypothesis. In this experiment participants were found to squeeze harder on high reward trials, however, this effect was limited to physical effort trials. No effect of increasing reward values on effort exertion during mental effort trials was observed. This difference in the pattern of results between mental and physical effort trials, along with the differences in mental and physical effort expenditure found when execution was immediate, suggests that mental and physical effort might be processed differently during Action Execution, contrary to H4, which states that they should be processed in a similar way.

As far as H5 is concerned, effort level was found to consistently determine the amount of effort exerted on each trial, suggesting that effort execution might be driven by effort requirements, rather than reward values. However, some indication that reward values might also be taken into account during Action Execution was provided by Experiment 5 as well, as participants were found to modulate their effort expenditure in response to reward values on the physical effort trials.

Contrary to H6, which states that different types of feedback should affect effort exertion differently, no effects of feedback type on effort expenditure were observed in this experiment.

Furthermore, results of Experiment 5 provide some evidence that delaying Action Execution does have an effect on effort exertion, in line with H7. This effect was found to depend on whether the effort required was mental or physical. On physical effort trials participants put in more effort (i.e. squeezed harder) when the experience of the outcome was delayed. On the mental effort trials, on the other hand, participants put in more effort (took longer to respond) when execution immediately followed choice.

5.1.6 Experiment 6 (PD study)

Experiment 6 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Group: PD vs. HC) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on grip strength (physical effort) and response times (mental effort) in PD patients and HCs.

These manipulations served to address the following hypotheses:

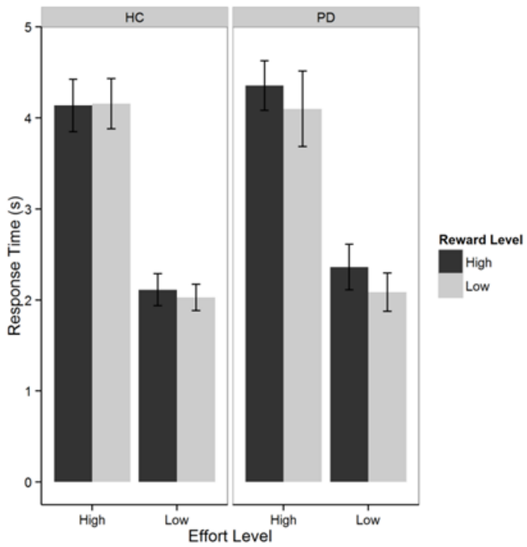
1) H1, which concerns the associations between relative reward values and effort,

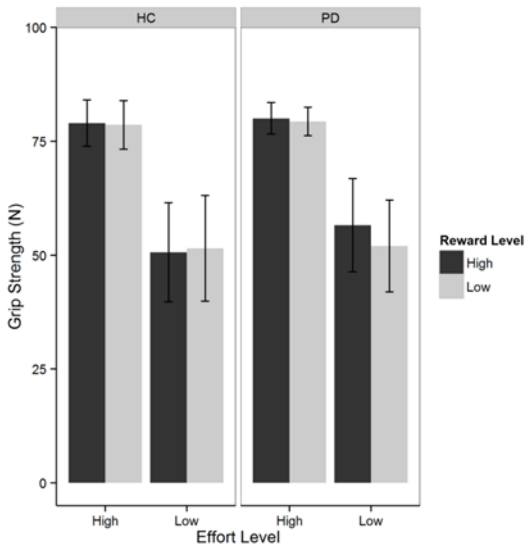
2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Execution,

4) H8, which concerns the effects of altered dopaminergic transmission on effort exertion.

Participants' performance on physical and mental effort trials is presented in Figure 17.





a) Response times on mental effort trials. *b)* Grip strength on physical effort trials.

Figure 17. Performance on mental (a) and physical (b) effort trials in Experiment 6.

Physical Effort

Analysis of grip strength during physical effort trials revealed a significant main effect of Effort Level ($\chi^2(1)=108.58$, p<0.001), with participants squeezing harder on High Effort trials compared to Low Effort trials (β=-56.17, *SE*=3.82, *t*(88.01)=-14.7, *p*<.001).

Mental Effort

Analysis of response times during mental effort trials revealed significant main effects of Effort Level ($\chi^2(2)=262.08$, *p*<.001) and Reward Level ($\chi^2(2)=11.45$, *p*=.003). Interaction between Effort Level and Reward Level was found to be significant as well ($\chi^2(1)=4.53$, *p*=.03).

In general participants were found to be slower on High Effort trials compared to Low Effort trials (β=.68, *SE*=.02, *t*(87.36)=40.31, *p*<.001) and High Reward trials compared to Low Reward trials (β=.04, *SE*=.02, *t*(87.36)=2.62, *p*=.01).

Post hoc comparisons using Tukey HSD test indicated that participants were significantly slower on High Reward trials compared to Low Reward trials when effort was low (β=.08, *SE*=.02, *t*(87.11)=3.42, *p*=.005), but not when it was high (*p*=.99). Participants were also significantly slower when the effort was high on both High Reward (β=.65, *SE*=.02, *t*(87.11)=27.50, *p*<.001) and Low Reward trials (β=.72, *SE*=.02, *t*(87.60)=29.48, *p*<.001).

Physical vs. Mental Effort

Participants on the mental effort trials were found to modulate their effort exertion in response to reward values. No such effect was found on the physical effort trials, suggesting that mental and physical effort might be processed differently during Action Execution.

Discussion

In general, the results of Experiment 6 suggest that: 1) increasing relative reward values leads to increased effort expenditure, but only on mental effort trials 2) mental and physical effort seem to be processed differently during Action Execution, 3) effort exertion is driven by effort requirements, 4) dopamine might not be crucial for energizing effort exertion during Action Execution.

More specifically, Experiment 6 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H4, H5, and H8. Results of Experiment 1 seem to support H1, which states that increasing reward values should lead to increased effort expenditure, as participants were found to put in more effort when rewards were higher on the mental effort trials. However, no such effects were observed on the physical effort trials, suggesting that effects of rewards are different depending on the type of effort required. Differences in behaviour on mental and physical effort trials in this experiment also suggest that these two types of effort might be processed differently during Action Execution, contrary to H4, which asserts that they should be processed in a similar way.

As far as H5 is concerned, results of this experiment suggest that effort exertion is driven primarily by effort requirements of a task, as participants were consistently found to exert more effort on high effort trials. Even though rewards were also shown to energize effort in certain circumstances (i.e. when mental effort was required) in this experiment, their effect seemed to differ depending on whether the effort required is mental or physical.

Furthermore, contrary to the hypothesis that effort exertion during Action Execution would be reduced in PD patients due to decreased levels of dopamine in this population (H8), no differences between PD patients and HCs on both mental and physical effort trials were found. This suggests that dopamine's role during Action Execution is not as pronounced as assumed by the V-E-D-M model.

5.2 General discussion

The V-E-D-M model assumes that manipulating effort, reward, and feedback characteristics during an effort-based decision-making task should lead to changes in the amount of effort people exert to obtain rewards. To investigate this assumption, the exact effects of these different manipulations on effort expenditure were examined in six experiments described in this chapter. Six areas of interest derived from the V-E-D-M model were investigated in these experiments: 1) Reward manipulations, 2) Effort manipulations, 3) Importance of effort/reward during Action Selection and Action Execution, 4) Outcome feedback, 5) Delayed Action Execution, 6) Neural underpinnings.

The rest of this chapter will survey the general pattern of findings across the six experiments with respect to the six areas of interest listed above, describing the implications of these findings for the assumptions of the V-E-D-M model.

1) Reward manipulations

a) Effects of manipulating reward magnitude on effort exertion

One of the assumptions that the V-E-D-M model makes is that increasing reward magnitude should have an impact on the amount of effort people put in during an effort-based decision-making task. The results of the experiments described above provide limited support for this assumption. In three out of six experiments (Experiments 1, 3, and 4) no effects of increased relative reward values on effort exertion were observed. In the remaining three experiments the effects of increasing reward values differed depending on whether the effort required was mental or physical. Increasing absolute reward values was also found to have a limited effect on performance. Taken together, these results suggest that neither relative nor absolute reward values have a reliable effect on effort expenditure during Action Execution. Most of the time people seem not to take reward values into account when modulating effort exertion. When people do take them into account, the effect of reward values is mediated by specific task characteristics such as the type and the amount of effort required within a task.

b) Effects of manipulating reward valence on effort exertion

According to the V-E-D-M model exerting effort to avoid losing money should differ from exerting effort to obtain monetary rewards. More specifically, people facing losses should increase their effort exertion if they are risk averse and want to minimize the chances of potential loss. This assumption was investigated in Experiment 2. In this experiment participants in the Loss group were found to be willing to put in additional mental effort to minimize the risk of incurring losses, in line with the assumption of the V-E-D-M model. No such effect was found on physical effort trials, however, which suggests that processing of physical effort might be less sensitive to losses than processing of mental effort, at least during Action Execution.

c) Effects of manipulating reward reliability on effort exertion

Another assumption that V-E-D-M model makes is that changing the reward reliability should have an influence on effort exerted during a task, with people exerting more effort when the probability of obtaining a reward is higher. No support for this hypothesis was found in the two experiments designed to test this assumption, as reward reliability was found not to have any effect on the amount of effort invested in the task.

2) Effort manipulation

The implicit assumption the V-E-D-M model makes is that mental and physical effort are processed in the same way throughout the stages of effort-based decision-making. This means that all the manipulations which affect one type of effort should affect the other type of effort in a similar way. This was not found to be the case across the experiments presented in this chapter. In general mental effort was found to be more sensitive than physical effort to reward manipulations such as increasing the absolute reward magnitude or changing the reward valence. Mental effort was also found to increase when execution immediately followed choice, as opposed to physical effort which was found to increase when execution was delayed. Taken together, this pattern of results suggests that mental effort and physical effort might be processed differently during Action Execution, contrary to the assumptions of the V-E-D-M model.

3) Importance of effort/reward during Action Selection and Action Execution

According to the V-E-D-M model, effort exerted during a task should be driven either by the reward values or by the effort requirements of this task. Experiments described in this chapter were designed to investigate which one of these two factors plays a bigger role during Action Execution. The results suggest that, even though reward often influences effort levels, during Action Execution effort exertion is driven predominantly by effort requirements. This result is in line with the theory of motivation by Brehm and Self (1989), which states that as long as the rewards are deemed to be worth the effort required, effort exerted during a task should be proportional to task demands, not the reward values.

4) Outcome feedback

The V-E-D-M model assumes that different types of reward feedback should influence effort exertion during effort-based decision-making task differently. However, no effects of different types of feedback were found in the experiments that explored this hypothesis. This result suggests that effort exertion is not sensitive to the feedback manipulations described in this thesis.

5) Delayed Action Execution

According to the V-E-D-M model, Learning is an important stage of the decision-making process, as it allows for updating the representations of the options available in a particular decision-making scenario. For that reason, preventing learning can potentially have important consequences for the future decisions made in similar circumstances. It can also influence the amount of effort people put in during an effort-based decision-making task. This assumption has been supported by the results of Experiment 5, which found that preventing immediate execution of an action after a choice was made affected the amount of effort exerted during the task. Nevertheless, delaying Action Execution seemed to result in a different pattern of behaviour for mental and physical effort trials. Delaying effort exertion was found to increase effort produced on the physical effort trials, but decrease effort put in on the mental effort trials. Possible explanations of this phenomenon are discussed in the general discussion in Chapter 7.

6) Neural underpinnings

Previous studies on the role of dopamine during effort exertion have suggested that this neurotransmitter is crucial for invigorating behaviour when effort is required. For this reason, one of the assumptions of the V-E-D-M model is that depleting dopamine levels should lead to decreased effort exertion during Action Execution stage of effort-based decision-making. The investigation of PD patients' performance on the effort-based decision-making task described in this chapter, however, does not support this hypothesis. PD patients were found to perform just as well as HCs on this task, putting in the same amount of effort. This result suggests that intact dopamine transmission might not be crucial for effort exertion.

Nevertheless, the fact that PD patients were tested on medication may potentially prevent any strong conclusions being drawn from this result.

5.3 Summary

Results of the studies presented above support some of the key hypotheses of the V-E-D-M model, for example regarding the effects of changing reward valence, or delaying action execution. They also help to clarify certain assumptions of the model, for example regarding the influence of reward values or different types of outcome feedback on effort exertion. Nevertheless, looking at grip strength and response times provides only partial information about effort expenditure during a task. To complete the picture of the effects of different manipulations on effort exertion, the accuracy of participants should be examined as well. Therefore, in the next chapter the effects of changing reward magnitude, valence, and reliability, as well as effort type and feedback on accuracy during Action Execution will be examined, to provide further information regarding the assumptions of the V-E-D-M model.

CHAPTER 6: Experimental Studies - Accuracy

Investigations of the choices people make and effort they put in during effort-based decision-making tasks provide an important source of information about the mechanisms of effort-based decision-making and validity of the V-E-D-M model, as demonstrated in Chapters 4 and 5. Another measure which has been commonly used to investigate effort exertion during effort-based decision-making tasks is participants' accuracy. The rationale for employing this measure is as follows: during most effort-based decision-making tasks the goal of participants is to maximize rewards obtained from the task. To achieve this goal, participants should recruit more effort when rewards at stake are higher, to increase their chances of obtaining these rewards. Increased effort exertion during effort-based decision-making task should, in turn, translate into increased accuracy. This means that investigating participants' accuracy can provide additional information about effort exerted during a task. For that reason participants' accuracy in the six experiments described in the previous chapters was analysed. These investigations covered six specific areas: 1) **Reward manipulations,** 2) **Effort manipulations,** 3) **Importance of effort/reward during Action Selection and Action Execution,** 4) **Outcome feedback,** 5) **Delayed Action Execution,** 6) **Neural underpinnings.**

As far as **Reward manipulations** are concerned, in this chapter the effects of a) increasing relative as well as absolute reward values, b) changing reward valence (from gain to loss), and c) changing reward reliability on participants' accuracy were examined. Furthermore, participants' accuracy on mental and physical effort trials was compared, to investigate **Effort manipulations**. **Importance of effort/reward during Action Execution** was also examined through investigating participants' accuracy on trials associated with different levels of effort and reward. The effects of different types of **Outcome feedback,** as well as the effects of **Delaying Action Execution** on participants accuracy were explored as well. Finally, the role of dopamine during Action Execution stage was investigated, in an effort to explore the **Neural underpinnings** of effort-based decision-making.

These topics were investigated in six studies which used the novel effort-based decision-making task described in Chapter 3. This task consisted of three phases: Training phase, Choice phase, and Execution phase. This chapter focuses specifically on participants' accuracy during the Execution phase. During this phase participants were asked squeeze a hand grip device (physical effort trials) or solve simple mathematical equations (mental effort trials) to obtain small monetary rewards (see Figure 11). To successfully complete physical effort trials participants had to reach a specific grip strength threshold. On high effort trials it was equivalent to 75N (Experiments 1-5) or 60% of maximum grip strength (Experiment 6). On low effort trials it was equivalent to 15N (Experiments 1-5) or 15% of maximum grip strength (Experiment 6). Participants were considered to be accurate on the physical effort trials when they managed to maintain their grip strength above the threshold level for 4.5s (Experiments 1-5) or 6s (Experiment 6). To successfully complete mental effort trials, on the other hand, participants had to solve all of the mathematical equations appearing on the screen. On high effort trials participants had to solve three equations, whereas on low effort trials they had to solve one equation. Participants were considered to be accurate on the mental effort trials when they managed to solve correctly all of the equations on the screen within 4.5s (Experiments 1-5) or 6s (Experiment 6). Participants' accuracy was analysed using GLMM assuming binomial distribution. The results of these analyses are presented in this chapter. The specific hypotheses investigated were:

H1: Increasing incentives available in a task should increase participants' accuracy on mental and physical effort trials.

H2: Participants in the Loss group should be more accurate than participants in the Gain group.

H3: Positive relationship between the probability of obtaining rewards and accuracy should be observed.

H4: Participants equally accurate on mental and physical effort trials.

H5: If behaviour during Action Execution is driven by reward values, accuracy levels should be proportional to the amount of reward available during a trial. If, however, it is driven by effort requirements, accuracy should mainly be determined by the amount of effort required.

H6: Type of feedback present during a task should have an effect on accuracy, with participants being most accurate on cumulative feedback trials, followed by discreet and simple feedback trials.

H7: Participants experiencing the outcome of their decisions immediately should achieve different levels of accuracy than participants executing their decisions after a delay.

H8: Depletion of dopamine levels in the brain associated with PD should lead to reduced accuracy on mental and physical effort trials.

The next section of this chapter describes the results of studies examining these eight hypotheses and discusses their implications for the V-E-D-M model.

Summary of the findings of different experiments is presented in Table 7.

Table 7. Results of the analyses of accuracy during six main experiments with regard to the 8 hypotheses investigated. “+” represents hypothesis supported by the results of the experiment, “-“ represents hypothesis for which support was not found, “partial“ represents hypothesis for which partial support was found, "?" represents inconclusive results. In column H5, the factor which was found to drive behaviour during effort exertion is specified.

Experiment	**Hypotheses**							
	H1 Effects of manipulating reward magnitude	**H2** Effects of manipulating reward valence	**H3** Effects of manipulating reward reliability	**H4** Comparison of mental/physical effort	**H5** Reward/Effort driving behaviour	**H6** Effects of manipulating reward feedback	**H7** Effects of immediate/delayed execution	**H8** Effects of dopamine depletion
Experiment 1 (Gains)	partial			?	effort/reward	-		
Experiment 2 (Losses)	partial	partial		?	effort/reward			
Experiment 3 (Reliability)	partial		-	?	effort/reward			
Experiment 4 (Increased Incentives)	relative: partial absolute: +		partial	?	effort/reward			
Experiment 5 (Immediate Execution)	partial			?	effort/reward	-	partial	
Experiment 6 (PD study)	partial			?	effort/reward			-

6.1 Results

In each of the following sections experimental design is described first, followed by the results from the physical effort trials, mental effort trials, and the comparison of the two types of trials. At the end of each section the findings are discussed in the context of the experimental hypotheses.

Participants' accuracy on different types of trials in the six experiments is presented in Appendix B.

6.1.1 Experiment 1 (Gains)

Experiment 1 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Physical vs. Mental) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on participants' accuracy during physical and mental effort trials. Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Execution,

4) H6, which concerns the effects of different types of feedback on accuracy.

Participants' accuracy on physical and mental effort trials is presented in Figure 18.

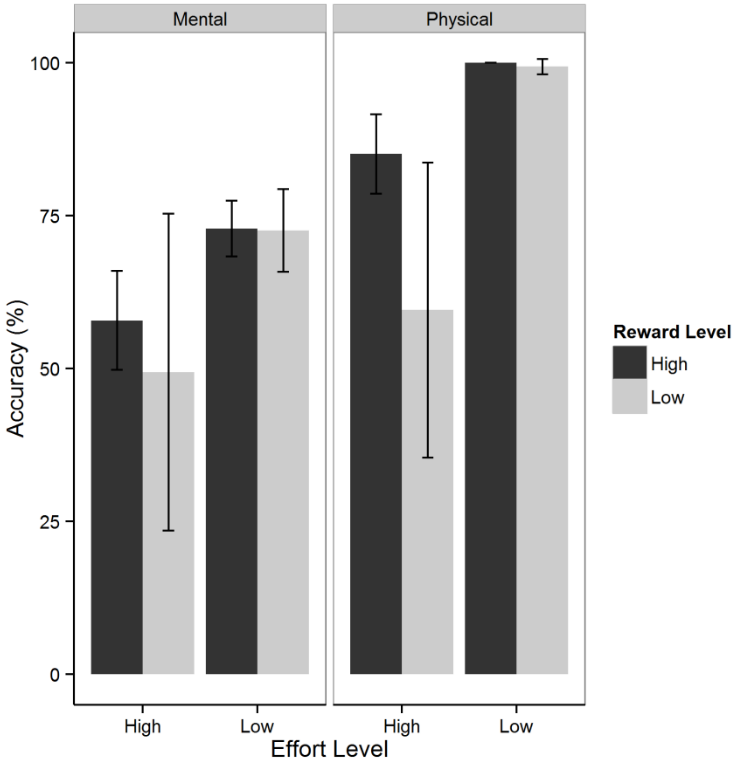


Figure 18. Accuracy during mental and physical effort trials in Experiment 1.

Physical Effort

Analysis of accuracy during physical effort trials revealed significant main effects of Effort Level ($\chi^2(1)=122.09$, $p<.001$) and Reward Level ($\chi^2(1)=18.21$, $p<.001$).

Participants were found to be more accurate on Low Effort compared to High Effort trials ($\beta=6.20$, $SE=1.12$, $z=5.52$, $p<.001$), and more accurate on High Reward compared to Low Reward trials ($\beta=2.11$, $SE=.50$, $z=4.21$, $p<.001$).

Mental Effort

Analysis of accuracy during mental effort trials revealed a significant main effect of Effort Level ($\chi^2(1)=21.79$, $p<.001$). Participants were found to be more accurate on Low Effort trials than on High Effort trials ($\beta=.68$, $SE=.15$, $z=4.67$, $p<.001$).

Physical vs. Mental Effort

Comparison of accuracy on mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(3)=311.74$, $p<.001$), as well as significant interactions between Effort Type and Effort Level ($\chi^2(1)=59.20$, $p<.001$), and Effort Type and Reward Level ($\chi^2(1)=5.73$, $p=.02$).

In general, participants were found to be more accurate on physical effort trials than on mental effort trials ($\beta=3.07$, $SE=.52$, $z=5.92$, $p<.001$).

Further post hoc comparisons using Tukey HSD test indicated that participants were more accurate on physical effort trials than on mental effort trials specifically when the effort required was low ($\beta=5.37$, $SE=1.01$, $z=5.34$, $p<.001$), but not high ($p=.09$). Furthermore, participants were found to be more accurate on Low Effort compared to High Effort trials when effort required was mental ($\beta=.70$, $SE=.26$, $z=2.74$, $p=.03$) as well as physical ($\beta=5.31$, $SE=1.04$, $z=5.11$, $p<.001$). Participants were as accurate on low mental effort trials as on high physical effort trials ($p=.99$). They were also less accurate on these two types of trials than on the low physical effort trials (low mental effort: $\beta=5.42$, $SE=1.01$, $z=5.36$, $p<.001$; high physical effort: $\beta=5.48$, $SE=1.04$, $z=5.28$, $p<.001$)

As far as the interaction between Effort Type and Reward Level is concerned, further analyses revealed that participants were more accurate on High Reward than on Low Reward trials when effort required was physical ($\beta=1.52$, $SE=.51$, $z=2.95$, $p=.02$), but not mental ($p=.99$). Participants were also found to be more accurate on physical effort trials compared to mental effort trials when reward was high ($\beta=3.85$, $SE=.56$, $z=6.87$, $p<.001$), as well as low ($\beta=2.29$, $SE=.65$, $z=3.50$, $p=.003$).

Discussion

In general, the results of Experiment 1 suggest that: 1) increased reward values can translate into higher accuracy in certain circumstances (e.g. when effort required is physical), 2) mental and physical effort tasks differed in difficulty, which has implications for interpretation of any differences between these two types of effort found in this experiment, 3) accuracy is sensitive to effort requirements and, in certain circumstances (e.g. when effort is physical) to reward values, and 4) feedback does not influence accuracy.

More specifically, Experiment 1 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H4, H5 and H6. According to H1, increasing the incentive value should increase participants' accuracy. This was indeed the case on the physical effort trials, where participants were found to be more accurate when high rewards were at stake.

However, no such effect was observed during mental effort trials. This suggests that the effects of rewards on accuracy are limited.

Furthermore, the results of Experiment 1 indicated that mental effort trials were possibly more difficult than physical effort trials, contrary to H4, which states that accuracy on mental and physical effort trials should be similar. Participants were found to be more accurate on physical effort trials compared to mental effort trials. The implications of this finding are discussed in the general discussion in Chapter 7.

Results of Experiment 1 also provide some indication that effort requirements drive accuracy during Action Execution (H5), as participants were consistently found to be significantly more accurate on low effort than high effort trials in this experiment. Furthermore, results suggest that reward values can impact accuracy as well, as participants were found to be more accurate on high reward than low reward trials when effort required was physical. Nevertheless, the effect of rewards was not reliable, as they seemed to have no effect on accuracy during the mental effort trials.

Contrary to H6, which states that different types of feedback should affect accuracy differently, the type of feedback presented during the task was found not to have any effect on accuracy during the task, providing further evidence that the effects of feedback on effort-based decision-making might be less pronounced than assumed by the V-E-D-M model.

6.1.2 Experiment 2 (Losses)

Experiment 2 was a 2 (Effort Level: High vs. Low) x 2 (Stakes Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Reward Valence: Gain vs. Loss) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low stakes on accuracy during mental and physical effort trials in two groups of participants: one trying to win monetary rewards (Gain group: participants from Experiment 1) and one trying to avoid losing them (Loss group). As described in section 5.1.2, in this experiment the effects of different stakes, rather than rewards, were examined. Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H2, which concerns the effects of gains and losses,

3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Execution,

5) H6, which concerns the effects of different types of feedback on accuracy.

Since participants in the Cumulative feedback condition did not choose any options associated with high effort and a potential loss of 15p, feedback had to be removed from the analyses in this experiment, as otherwise the model would not converge due to zero cell counts for categorical predictors.

Participants' performance on physical and mental effort trials in Experiment 2 is presented in Figure 19.

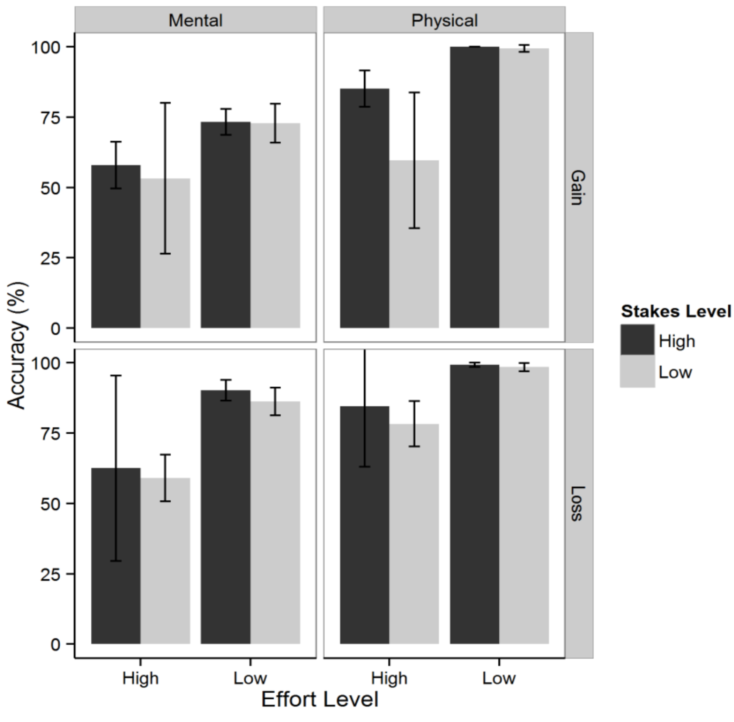


Figure 19. Accuracy during mental and physical effort trials in Experiment 2.

Physical Effort

Analysis of participants' accuracy on physical effort trials revealed significant main effects of Effort Level ($\chi^2(3)$=244.19, p<.001), Stakes Level ($\chi^2(3)$=19.74, p<.001), and Reward

Valence (χ^2(3)=13.67, *p*=.003), as well as a significant interaction between Reward Valence and Effort Level (χ^2(1)=9.86, *p*=.002).

In general, participants were found to be more accurate on Low Effort than High Effort trials (β=4.79, *SE*=.67, *z*=7.11, *p*<.001). Participants were also found to be more accurate on High Stakes trials than Low Stakes trials (β=1.40, *SE*=.42, *z*=3.37, *p*<.001). Participants in the Loss group were found to be as accurate as participants in the Gain group (*p*=.24).

Further post hoc comparisons using Tukey HSD test indicated that participants were more accurate on Low Effort trials compared to High Effort trials in both Gain (β=6.28, *SE*=1.16, *z*=5.44, *p*<.001) and Loss (β=3.30, *SE*=.52, *z*=6.35, *p*<.001) groups. Participants in the Loss group were as accurate as participants in the Gain group during both High Effort (*p*=.64) and Low Effort (*p*=.20) trials.

Mental Effort

Analysis of accuracy during mental effort trials revealed significant main effects of Effort Level (χ^2(3)=93.08, *p*<.001) and Reward Valence (χ^2(3)=29.1, *p*<.001). Interactions between Reward Valence and Effort Level (χ^2(1)=4.60, *p*=.03) and Reward Valence and Stakes Level (χ^2(1)=4.45, *p*=.03) were also found to be significant.

In general, participants were found to be more accurate on Low Effort than High Effort trials (β=1.13, *SE*=.12, *z*=9.31, *p*<.001). Participants in the Loss group were also found to be more accurate than participants in the Gain group (β=.66, *SE*=.25, *z*=2.60, *p*=.009).

Post hoc comparisons using Tukey HSD test indicated that participants in the Loss group were significantly more accurate on Low Effort trials (β=1.09, *SE*=.22, *z*=4.88, *p*<.001), but not High Effort trials (*p*=.94), compared to participants in the Gain group. Participants in both Gain (β=.70, *SE*=.22, *z*=3.18, *p*=.008) and Loss (β=1.56, *SE*=.25, *z*=6.33, *p*<.001) groups were significantly more accurate on Low Effort trials compared to High Effort trials.

Furthermore, participants in the Loss experiment were found to be significantly more accurate on High Stakes trials than participants in the Gain group (β=.97, *SE*=.30, *z*=3.18, *p*=.008).

Physical vs. Mental Effort

Comparison of accuracy during mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(10)=445.8$, $p<.001$), as well as significant interactions between Effort Type and Effort Level ($\chi^2(4)=82.30$, $p<.001$), Effort Type and Stake Level ($\chi^2(4)=14.22$, $p=.006$), Effort Type and Reward Valence ($\chi^2(6)=40.12$, $p<.001$), Effort Type, Reward Valence and Effort Level ($\chi^2(2)=12.19$, $p=.002$), and Effort Type, Reward Valence and Stakes Level ($\chi^2(2)=7.57$, $p=.02$).

In general, participants were found to be more accurate on the physical effort trials compared to the mental effort trials ($\beta=2.35$, $SE=.29$, $z=8.12$, $p<.001$).

Further analyses revealed that participants in the Loss group were more accurate on the physical compared to mental effort trials when effort was high ($\beta=.98$, $SE=.21$, $z=4.70$, $p<.001$) as well as low ($\beta=2.40$, $SE=.32$, $z=7.47$, $p<.001$). Participants in the Gain group, on the other hand, were found to be more accurate on the physical compared to mental effort trials when effort was low ($\beta=5.43$, $SE=1.01$, $z=5.36$, $p<.001$), but not high ($p=.25$).

Furthermore, participants in the Gain group were found to be more accurate on High Stakes trials compared to Low Stakes trials when effort required was physical ($\beta=1.81$, $SE=.48$, $z=3.78$, $p<.001$), but not mental ($p=.93$).

Finally, participants in both Gain and Loss groups were found to be more accurate on high physical ($\beta=.77$, $SE=.22$, $z=3.51$, $p=.002$) and low mental effort trials ($\beta=1.14$, $SE=.12$, $z=9.35$, $p<.001$) than on high mental effort trials. At the same time they were found to be less accurate on these two types of trials than on the low physical effort trials (high physical effort: $\beta=-4.30$, $SE=.60$, $z=-7.16$, $p<.001$; low mental effort: $\beta=-3.93$, $SE=.55$, $z=-7.11$, $p<.001$). They were also found to achieve a similar level of accuracy on high physical and low mental effort trials ($p=.29$), as indicated by Figure 19.

Discussion

In general, the results of Experiment 2 suggest that: 1) increasing the monetary stakes can lead to increased accuracy in certain circumstances (e.g. when physical effort is required), 2) when losses are a possibility accuracy can increase in certain circumstances (e.g. when mental effort is required), 3) mental and physical effort tasks differed in difficulty, 4) accuracy is driven primarily by effort requirements, but reward values can affect it as well in certain circumstances (e.g. when effort required is physical).

More specifically, Experiment 2 was set up to investigate five hypotheses derived from the V-E-D-M model: H1, H2, H4, H5, and H6. In line with H1, it was predicted that participants in this experiment would be more accurate on trials associated with high stakes (15p win or 15p loss), than on trials associated with low stakes (5p win or 5p loss). This was, however, observed on the physical effort trials only. On the mental effort trials participants were just as accurate regardless of whether stakes were high or low. This suggests that rewards have a limited effect on accuracy.

As far as H2 is concerned, which states that participants in the Loss group should be more accurate than participants in the Gain group, only partial support for this hypothesis was found, as no differences in accuracy between Loss and Gain groups were observed on the physical effort trials. On the mental effort trials, participants in the Loss group were found to be more accurate than participants in the Gain group when effort required was low and when the stakes were high. These results suggest that participants in the Loss group were trying harder to be accurate during mental effort trials, especially when trying to avoid high losses, which suggests that they were more risk averse than participants in the Gain group during these trials.

In addition, results of Experiment 2 suggest that mental effort trials were more difficult to complete than physical effort trials, contrary to H4, as participants were found to be significantly less accurate on mental than on physical effort trials during this experiment.

Furthermore, results of this experiment suggest that effort requirements are the main factor driving accuracy during effort-based decision-making tasks (H5), as participants were consistently found to be more accurate on low effort than high effort trials. In addition, reward values were also found to affect accuracy in certain circumstances, as participants were found to be more accurate on high stakes compared to low stakes trials, but only when the effort required was physical.

6.1.3 Experiment 3 (Reliability)

Experiment 3 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 3 (Reward Reliability: Deterministic vs. Probabilistic vs. Unreliable) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on accuracy during mental and physical effort trials in three groups: Deterministic (reward present on 100% of successful trials), Probabilistic (reward present on 75% of successful trials and 25% of unsuccessful trials), or Unreliable (reward present on 50% of the trials, regardless of whether they were successful or not).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H3, which concerns the effects of reward reliability,

3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Execution.

Participants' performance on physical and mental effort trials in Experiment 3 is presented in Figure 20.

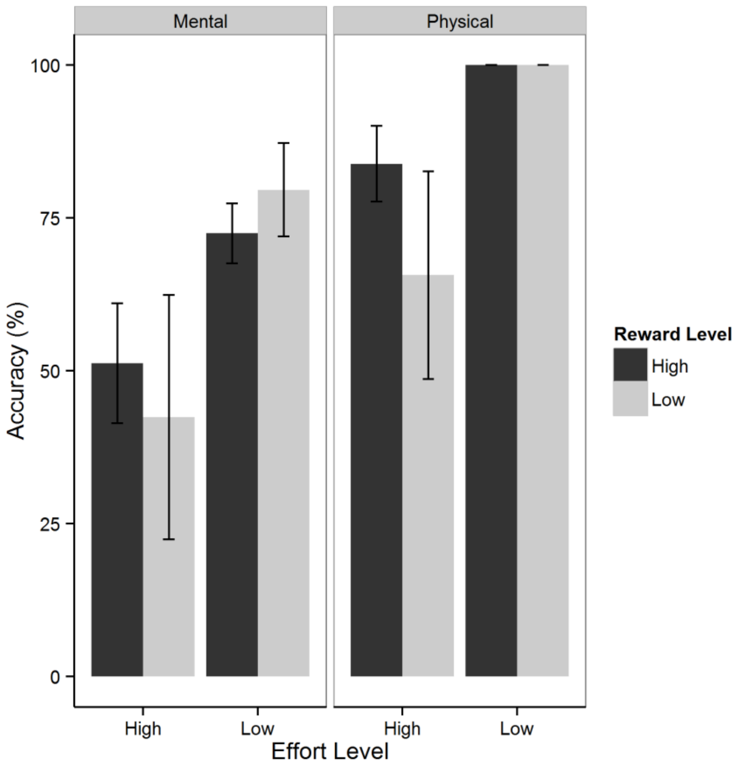


Figure 20. Accuracy during mental and physical effort trials in Experiment 3.

Physical Effort

Preliminary analysis of accuracy during physical effort trials revealed that participants were 100% correct on low effort trials (see Appendix B). Consequently there was too little variability in their responses to include low effort trials into further analysis. For that reason the results described below refer to high physical effort trials only.

When investigating accuracy on high physical effort trials, main effect of Reward Level was found to be significant ($\chi^2(1)=15.45$, $p<.001$). Participants were found to be significantly more accurate when reward was high ($\beta=1.44$, $SE=.37$, $z=3.85$, $p<.001$).

Mental Effort

Analysis of accuracy during mental effort trials revealed a significant main effect of Effort Level ($\chi^2(1)=27.61$, $p<.001$). Participants were found to be significantly more accurate when effort was low ($\beta=1.25$, $SE=.002$, $z=704.60$, $p<.001$).

Physical vs. Mental Effort

Comparisons of participants' accuracy during mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(2)=357.19$, $p<.001$), and an interaction between Effort Type and Effort Level ($\chi^2(1)=51.76$, $p<.001$).

In general, participants were found to be significantly more accurate on the physical effort trials compared to the mental effort trials ($\beta=2.33$, $SE=.15$, $z=15.02$, $p<.001$).

Post hoc comparisons using Tukey HSD test revealed that participants were more accurate on Low Effort than High Effort trials when the effort required was mental ($\beta=1.44$, $SE=.18$, $z=7.90$, $p<.001$). The significance of the difference in accuracy between high and low physical effort trials could not be established, due to the lack of variability in the data from the low physical effort trials. However, visual inspection of Figure 20 suggests that participants were more accurate on Low Effort compared to High Effort trials when the effort required was physical. Participants were also significantly more accurate on high physical effort trials compared to high mental effort trials ($\beta=1.72$, $SE=.17$, $z=9.88$, $p<.001$). Participants' accuracy was similar on low physical effort trials and high mental effort trials ($p=.44$).

Discussion

In general, the results of Experiment 3 suggest that: 1) increasing monetary rewards can lead to increased accuracy in certain circumstances (e.g. when physical effort is required), 2) reward reliability does not influence accuracy, 3) mental and physical effort tasks differed in difficulty, 4) accuracy is driven primarily by effort requirements, but reward values can play a role as well in certain circumstances (e.g. when physical effort is required).

More specifically, Experiment 3 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H3, H4, and H5. As far as H1 is concerned, results of Experiment 3, in partial support of this hypothesis, show that increasing the incentive value can lead to increased accuracy in certain circumstances. Participants were found to be more accurate on high reward than low reward trials when effort required was physical, but not mental.

Furthermore, in Experiment 3 no relationship between reward reliability and accuracy was observed, contrary to H3, which states that accuracy should increase in line with reward reliability. This, in turn, suggests that that the probability of obtaining rewards does not affect participants' accuracy during effort-based decision-making tasks.

In addition, differences in accuracy on mental and physical effort trials were observed in this experiment, contrary to H4, which assumes that mental and physical effort are processed in the same way. In general, participants were found to be less accurate on mental effort trials than on physical effort trials. This suggests that mental effort trials were more difficult for participants than physical effort trials. This finding is in line with the results of the previous experiments described in this chapter.

Finally, results of Experiment 3 suggest that effort requirements might be the main determinant of participants' accuracy during effort-based decision making tasks (H5), as participants were consistently found to be more accurate on low effort trials compared to high effort trials in this experiment. Moreover, the findings from this experiment suggest that rewards might affect accuracy in certain circumstances as well. Participants were found to be more accurate when rewards were high compared to low on high physical effort trials.

6.1.4 Experiment 4 (Increased Incentives)

Experiment 4 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: High vs. Low) x 2 (Reward Magnitude: Large Rewards vs. Small Rewards) x 3

(Reward Reliability: Deterministic vs. Probabilistic vs. Unreliable) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on accuracy during mental and physical effort trials in two groups: one exerting effort for small rewards (15p and 5p) (Small Rewards group: participants from Experiment 1) and one exerting effort for large rewards (30p and 15p) (Large Rewards group). Participants were randomly assigned to one of the three groups: Deterministic (reward present on 100% of successful trials), Probabilistic (reward present on 75% of successful trials and 25% of unsuccessful trials), or Unreliable (reward present on 50% of the trials, regardless of whether they were successful or not).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative as well as absolute reward values and effort,

2) H3, which concerns the effects of reward reliability,

3) H4, which concerns the differences between mental and physical effort,

4) H5, which concerns the factors (reward/effort) driving Action Execution.

Participants' performance on physical and mental effort trials in Experiment 4 is presented in Figure 21.

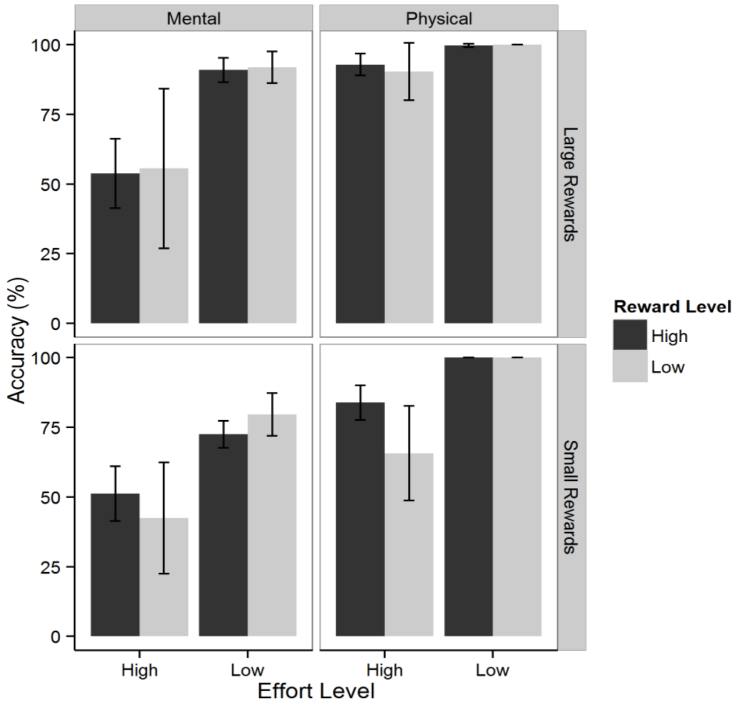


Figure 21. Accuracy during mental and physical effort trials in Experiment 4.

Physical Effort

Preliminary analysis revealed that participants were almost 100% accurate on low physical effort trials (see Appendix B), and so there was too little variability in the results to include low effort trials into further analyses. For that reason the results below refer to high physical effort trials only.

Analysis of participants' accuracy on the high physical effort trials revealed significant main effects of Reward Level ($\chi^2(1)=14.70$, $p<.001$) and Reward Magnitude ($\chi^2(1)=6.45$, $p=.001$).

Participants were found to be more accurate on High Reward trials than on Low Reward trials (β=.93, *SE*=.34, *z*=2.70, *p*=.007). Furthermore, participants in the Large Rewards group were found to be more accurate than participants in the Small Rewards group (β=1.10, *SE*=.43, *z*=2.58, *p*=.01).

Mental Effort

Investigations of accuracy on the mental effort trials revealed significant main effects of Effort Level ($\chi^2(6)=195.02$, $p<.001$), Reward Reliability ($\chi^2(4)=19.20$, $p<.001$) and Reward Magnitude ($\chi^2(4)=35.63$, $p<.001$). Interactions between Reward Magnitude and Effort Level

($\chi^2(2)=26.46$, $p<.001$), as well as Reward Reliability and Effort Level ($\chi^2(2)=13.54$, $p=.001$) were also significant.

In general, participants were found to be more accurate on Low Effort trials compared to High Effort trials (β=1.95, *SE*=.20, *z*=9.90, $p<.001$). In addition, participants in the Large Rewards group were found to be more accurate than participants in the Small Rewards group (β=.78, *SE*=.29, *z*=2.72, $p=.007$). No significant differences in accuracy between participants from Cumulative, Discreet, and Unreliable groups were observed ($p>.05$).

Post hoc comparisons using Tukey HSD test indicated that participants in the Large Rewards group were more accurate than participants in the Small Rewards group when the effort required was low (β=1.41, *SE*=.31, *z*=4.52, $p<.001$), but not high ($p=.97$). Participants in both Large Rewards group (β=2.57, *SE*=.33, *z*=7.78, $p<.001$) and Small Rewards group (β=1.32, *SE*=.21, *z*=6.37, $p<.001$) were also found to be more accurate on Low Effort trials than High Effort trials. Furthermore, Participants in the Probabilistic condition were significantly less accurate on high effort trials than participants in the Deterministic condition (β=-1.15, *SE*=.34, *z*=3.38, $p=.01$). No other comparisons were significant.

Physical vs. Mental Effort

Comparison of participants' accuracy during mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(8)=572.06$, $p<.001$). Interactions between Effort Type and Effort Level ($\chi^2(4)=70.18$, $p<.001$), Effort Type and Reward Magnitude ($\chi^2(2)=42.36$, $p<.001$), as well as Effort Type, Reward Magnitude and Effort Level ($\chi^2(2)=29.20$, $p<.001$) were also found to be significant.

In general, participants were found to be more accurate on physical effort trials than on mental effort trials (β=3.29, *SE*=.53, *z*=6.22, $p<.001$).

Further analyses revealed that participants in the Large Rewards group were more accurate on physical effort trials compared to mental effort trials (β=2.95, *SE*=.27, *z*=11.08, $p<.001$). Participants in the Small Rewards group were also found to be more accurate on physical effort trials than mental effort trials (β=1.73, *SE*=.18, *z*=9.87, $p<.001$), but only when the effort required was high. In this group accuracy on low physical effort trials could not be assessed, as all participants were found to be 100% accurate on these trials. Participants in both Large Rewards and Small Rewards groups were found to be more accurate on high physical (β=2.18, *SE*=.19, *z*=11.25, $p<.001$) and low mental effort trials (β=1.98, *SE*=.17, *z*=11.45, *p*<.001) than on high mental effort trials. They were also found to achieve a similar level of accuracy on high physical and low mental effort trials (*p*=.70), as indicated by Figure 21.

Discussion

In general, the results of Experiment 4 suggest that: 1) increasing both relative and absolute reward values can influence accuracy in certain circumstances (e.g. when effort required is physical), 2) Increasing reward reliability can lead to increased accuracy in certain circumstances (e.g. when effort required is mental), 3) mental and physical effort tasks differed in difficulty, 4) accuracy is driven primarily by effort requirements, but reward values can play a role as well in certain circumstances (e.g. when physical effort is required).

More specifically, Experiment 4 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H3, H4, and H5. As far as H1 is concerned, Experiment 4, in partial support of this hypothesis, showed that increasing relative values of rewards can affect accuracy in certain circumstances. Participants were found to be more accurate when rewards were high on high physical effort trials. No such effect was observed on mental effort trials. Increasing absolute reward values was also shown to impact accuracy in this experiment, as participants in the Large Rewards group were found to be more accurate than participants in the Small Rewards group on high physical effort trials and low mental effort trials. These results suggest that reward values have a potential to influence accuracy in certain circumstances.

Experiment 4 also provided some evidence that reward reliability might have an impact on accuracy, in line with H3, as during high mental effort trials participants in the Probabilistic condition were significantly less accurate than participants in the Deterministic condition.

Comparisons of accuracy during mental and physical effort trials were somewhat difficult due to the lack of variability in accuracy on low physical effort trials. In general, though, the results of Experiment 4 suggest that participants were more accurate on physical effort trials than on mental effort trials, contrary to H4, which predicted that there should be no differences between these two types of trials. This result implies that mental effort trials were more difficult for participants than physical effort trials.

Furthermore, results of Experiment 4 suggest that accuracy on effort-based decision-making tasks is primarily driven by effort requirements (H5), as participants were consistently found to be more accurate on trials which required less effort. Moreover, the findings from this experiment suggest that rewards might affect accuracy in certain circumstances as well. This is because participants were found to be more accurate when rewards were high compared to low on high physical effort trials.

6.1.5 Experiment 5 (Immediate Execution)

Experiment 5 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Timing of Execution: Immediate Execution vs. Delayed Execution) x 3 (Reward Feedback: Cumulative vs. Discreet vs. Simple) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on accuracy during mental and physical effort trials in two groups of participants: one required to execute their choices immediately after they were made (Immediate Execution group), and one executing their choices after a delay (Delayed Execution group: participants from Experiment 1). Participants were randomly assigned to one of the three Reward Feedback groups: Cumulative (accuracy feedback + reward received on a particular trial + reward accumulated so far), Discreet (accuracy feedback + reward received on a particular trial), or Simple (accuracy feedback).

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Execution,

4) H6, which concerns the effects of different types of feedback on effort exertion,

5) H7, which concerns the effects of delaying Action Execution.

Participants' performance on the physical and mental effort trials in Experiment 5 is presented in Figure 22.

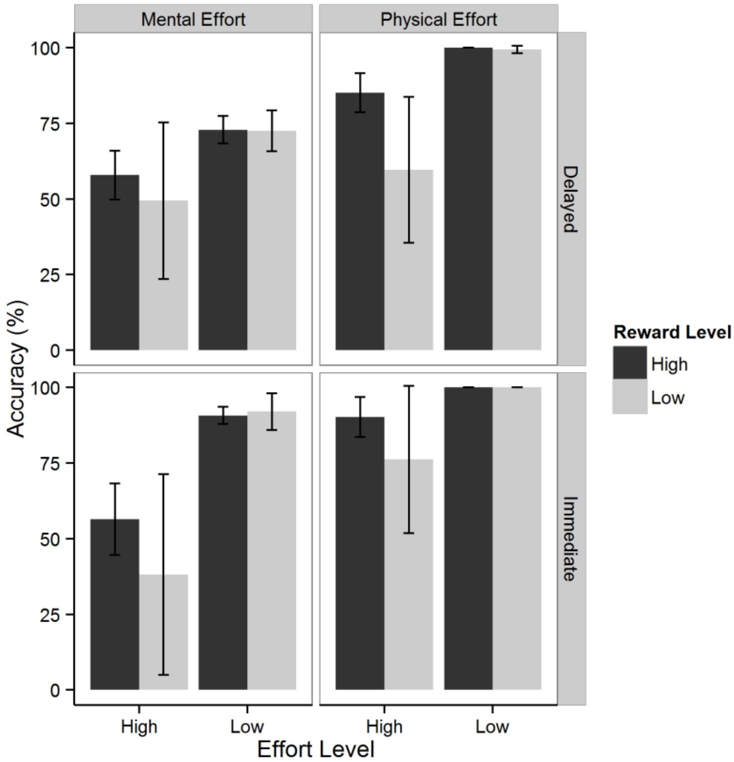


Figure 22. Accuracy during mental and physical effort trials in Experiment 5.

Physical Effort

Analysis of participants' accuracy during physical effort trials in Experiment 5 revealed significant main effects of Effort Level ($\chi^2(1)$=197.10, *p*<.001) and Reward Level ($\chi^2(1)$=20.44, *p*<.001).

Participants were found to be more accurate when effort was low (β=6.21, *SE*=1.07, *z*=5.83, *p*<.001), and when reward was high (β=1.77, *SE*=.38, *z*=4.62, *p*<.001).

Mental Effort

As far as the analysis of the accuracy on the mental effort trials is concerned, significant main effects of Effort Level ($\chi^2(3)$=150.27, *p*<.001) and Timing of Execution ($\chi^2(2)$=50.71, *p*<.001) were found. Interaction between Effort Level and Timing of Execution was also found to be significant ($\chi^2(1)$=41.00, *p*<.001).

In general, participants were found to be more accurate on Low Effort trials than on High Effort trials (β=1.64, *SE*=.20, *z*=8.15, *p*<.001). Participants in the Immediate Execution group were also found to be more accurate than participants in the Delayed Execution group (β=.63, *SE*=.21, *z*=3.06, *p*=.002).

Further analyses revealed that participants in the Immediate Execution group were more accurate than participants in the Delayed Execution group on Low Effort trials (β=1.42, *SE*=.27, *z*=5.21, *p*<.001), but not High Effort trials (*p*=.88). In addition, participants were significantly more accurate on Low Effort trials compared to High Effort trials in both Immediate (β=2.21, *SE*=.24, *z*=9.39, *p*<.001) and Delayed (β=.67, *SE*=.16, *z*=4.15, *p*<.001) execution groups.

Physical vs. Mental Effort

Comparison of accuracy during mental and physical effort trials revealed a significant main effect of Effort Type (χ^2(8)=523.38, *p*<.001), as well as interactions between Effort Type and Effort Level (χ^2(4)=102.50, *p*<.001), Effort Type and Reward Level (χ^2(2)=9.96, *p*=.007), Effort Type and Timing of Execution (χ^2(4)=51.82, *p*<.001), and Effort Type, Timing of Execution and Effort Level (χ^2(2)=39.54, *p*<.001).

In general, participants were found to be more accurate on the physical effort trials than on the mental effort trials (β=1.49, *SE*=.19, *z*=7.72, *p*<.001).

Further analyses revealed that participants in the Immediate Execution group were significantly more accurate on physical effort trials than on mental effort trials when effort required was high (β=2.37, *SE*=.25, *z*=9.36, *p*<.001). Participants in this group were also found to be significantly more accurate on Low Effort than High Effort trials when effort required was mental (β=2.78, *SE*=.30, *z*=9.39, *p*<.001). Unfortunately participants' accuracy on Low Effort physical trials in this group could not be investigated, as there was too little variability in performance on these trials (participants were almost 100% correct).

As far as the Delayed Execution group is concerned, no differences in accuracy between mental and physical effort trials were found when the effort required was high (*p*=.18). However, participants in this group were found to be significantly more accurate on physical effort trials compared to mental effort trials when effort required was low (β=5.42, *SE*=1.01, *z*=5.36, *p*<.001). Participants in this group were also found to be more accurate on Low Effort than High Effort trials when effort was mental (β=.68, *SE*=.24, *z*=2.85, *p*=.02) as well as physical (β=5.49, *SE*=1.04, *z*=5.29, *p*<.001). Furthermore, participants in the Delayed Execution group were found to be significantly more accurate on physical effort trials compared to mental effort trials when reward was high (β=3.94, *SE*=.56, *z*=6.99, *p*<.001) as well as low (β=2.08, *SE*=.62, *z*=3.36, *p*=.004). They were also more accurate on High Reward trials than Low Reward trials when effort required was physical (β=1.76, *SE*=.47, *z*=3.71, *p*=.001), but not mental (*p*=.98).

Finally, participants in both Immediate and Delayed Execution groups were found to be more accurate on high physical (β=1.34, *SE*=.24, *z*=5.66, *p*<.001) and low mental effort trials (β=1.62, *SE*=.20, *z*=8.24, *p*<.001) than on high mental effort trials. They were also found to achieve a similar level of accuracy on high physical and low mental effort trials (*p*=.50), as indicated by Figure 22.

Discussion

In general, the results of Experiment 5 suggest that: 1) increasing relative reward values can lead to increased accuracy in certain circumstances (e.g. when effort required is physical), 2) mental and physical effort tasks differed in difficulty, 3) accuracy is driven primarily by effort requirements, but reward values can play a role as well in certain circumstances (e.g. when effort required is physical), 4) feedback does not influence accuracy, and 5) immediate execution improves accuracy on low mental effort trials.

More specifically, Experiment 5 was designed to investigate five hypotheses derived from the V-E-D-M model: H1, H4, H5, H6, and H7. As far as H1 is concerned, the results of Experiment 5 indicate that increasing incentives available in a task can improve accuracy in certain circumstances, in partial support for this hypothesis, as participants were found to be more accurate when rewards were high on physical effort trials. However, no such effect was observed on mental effort trials.

This difference in the effect of rewards on mental and physical effort trials, along with differences in the effects of immediate or delayed execution on accuracy during mental and physical effort trials, suggest that mental and physical effort might be processed differently during Action Execution, contrary to H4, which states that they should be processed in a similar way. Furthermore, participants were found to be more accurate on physical effort trials compared to mental effort trials, which suggests that these trials were easier than mental effort trials.

The results of Experiment 5 also suggest that accuracy on effort-based decision-making tasks is primarily driven by effort requirements (H5), as participants were consistently found to be more accurate on trials which required less effort. Moreover, the findings suggest that rewards might affect accuracy in certain circumstances as well, as participants were found to be more accurate when rewards were high compared to low on high physical effort trials. Contrary to H6, which asserts that different types of feedback should affect accuracy differently, no effects of feedback type on accuracy were observed in this experiment.

In addition, results of Experiment 5 provide some evidence that delaying Action Execution can have an impact on accuracy in certain circumstances (H7). This is because participants in the Immediate Execution group were found to be more accurate on low mental effort trials than participants in the Delayed Execution group.

6.1.6 Experiment 6 (PD study)

Experiment 6 was a 2 (Effort Level: High vs. Low) x 2 (Reward Level: High vs. Low) x 2 (Effort Type: Mental vs. Physical) x 2 (Group: PD vs. HC) design. The critical manipulation was comparing the effects of high vs. low effort and high vs. low reward on accuracy during mental and physical effort trials in PD patients and HCs.

These manipulations served to address the following hypotheses:

1) H1, which concerns the associations between relative reward values and effort,

2) H4, which concerns the differences between mental and physical effort,

3) H5, which concerns the factors (reward/effort) driving Action Execution,

4) H8, which concerns the effects of altered dopaminergic transmission on effort exertion.

Participants' performance on the physical and mental effort trials in Experiment 6 is presented in Figure 23.

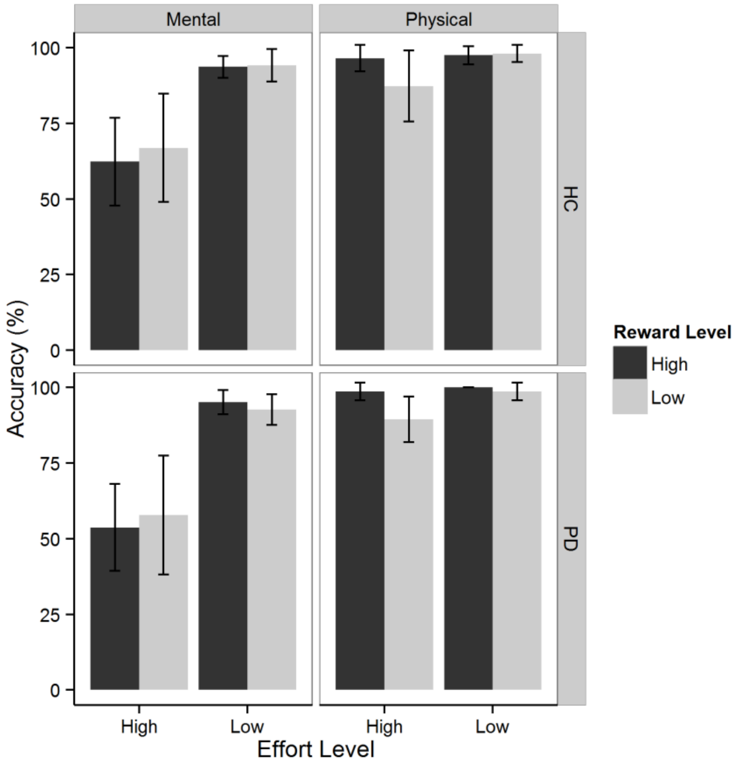


Figure 23. Accuracy during mental and physical effort trials in Experiment 6.

Physical Effort

Analysis of participants' accuracy on physical effort trials revealed significant main effects of Effort Level ($\chi^2(2)=18.01$, $p<.001$) and Reward Level ($\chi^2(2)=16.01$, $p<.001$).

Participants were found to be more accurate on High Reward trials than on Low Reward trials ($\beta=1.91$, $SE=.54$, $z=3.54$, $p<.001$). No significant differences in accuracy between high and low effort trials ($p=.30$) were found.

Mental Effort

Analysis of accuracy on mental effort trials revealed a significant main effect of Effort Level ($\chi^2(1)=174.79$, $p<.001$), as participants were found to be more accurate when effort was low ($\beta=2.65$, $SE=.24$, z=11.14, $p<.001$). No other significant effects were found.

Physical vs. Mental Effort

Comparison of accuracy during mental and physical effort trials revealed a significant main effect of Effort Type ($\chi^2(6)=189.15$, $p<.001$). Interaction between Effort Type and Reward Level ($\chi^2(2)=15.44$, $p<.001$) was also found to be significant.

In general, participants were found to be more accurate on physical effort trials than on mental effort trials (β=2.21, *SE*=.28, *z*=8.04, *p*<.001).

Further analyses showed that participants were more accurate on high (β=2.74, *SE*=.003, *z*=994.80, *p*<.001) and low (β=1.58, *SE*=.004, *z*=402.28, *p*<.001) reward trials when effort required was physical as compared to mental. They were also more accurate on High Reward trials compared to Low Reward trials when effort required was physical (β=1.19, *SE*=.004, *z*=300.67, *p*<.001) and when it was mental (β=.04, *SE*=.003, *z*=12.83, *p*<.001).

Finally, both PD patients and HCs were found to be more accurate on high physical (β=2.75, *SE*=.29, *z*=9.43, *p*<.001) and low mental effort trials (β=2.54, *SE*=.23, *z*=10.95, *p*<.001) than on high mental effort trials. At the same time they were found to be less accurate on these two types of trials than on the low physical effort trials (high physical effort: β=-1.47, *SE*=.48, *z*=-3.03, *p*=.01; low mental effort: β=-1.68, *SE*=.46, *z*=-3.66, *p*=.002). They were also found to achieve a similar level of accuracy on high physical and low mental effort trials (*p*=.92), as indicated by Figure 23.

Discussion

In general, results of Experiment 6 suggest that: 1) increasing relative reward values can lead to increased accuracy in certain circumstances (e.g. when effort required is physical), 2) mental and physical effort tasks differed in difficulty, 4) dopamine depletion in PD does not have a strong influence on accuracy during effort-based decision-making task, at least when patients are assessed on dopaminergic medication.

More specifically, Experiment 6 was designed to investigate four hypotheses derived from the V-E-D-M model: H1, H4, H5, and H8. As a far as H1 is concerned, results of this experiment indicated that increasing reward values can lead to increased accuracy in certain circumstances, in partial support of this hypothesis. Participants were found to be more accurate when rewards were high on physical effort trials. No such effect was observed on mental effort trials, however.

Furthermore, participants in Experiment 6 were found to be more accurate on physical effort trials compared to mental effort trials (H4), which suggests that physical effort trials were easier for them. This result replicates the findings of the previous experiments described in this chapter.

As far as H5 is concerned, results of this experiment suggest that both reward values and effort requirements can play a role when determining the accuracy of participants. More specifically, in this experiment reward values were found to be the factor driving accuracy during physical effort trials, whereas effort requirements drove accuracy during mental effort trials.

In line with the previous studies investigating the effects of dopamine on effort-based decision-making it was assumed that decreased levels of dopamine in PD patients would lead to decreased accuracy in this group in Experiment 6 (H8). However, no such effect was found, suggesting that accuracy is not as reliant on the dopamine levels in the brain as previously thought.

6.2 General discussion

When assessing the validity of the assumptions of the V-E-D-M model, different behavioural measures related to effort processing need to be investigated. One of these measures is accuracy, assumed to reflect the amount of effort invested in a task. In the six experiments described above participants' accuracy during the effort-based decision-making task was examined. Six areas of interest derived from the V-E-D-M model were investigated in these experiments: 1) Reward manipulations, 2) Effort manipulations, 3) Stages of decision-making, 4) Outcome feedback, 5) Delayed and immediate feedback, 6) Neural underpinnings.

The rest of this chapter will survey the general pattern of findings across the six experiments with respect to the six areas of interest listed above, describing the implications of these findings for the assumptions of the V-E-D-M model.

1) Reward manipulations

a) Effects of manipulating reward magnitude on accuracy

One of the assumptions of the V-E-D-M model is that increasing relative/absolute reward values in an effort-based decision-making task should translate into increased effort exertion and consequently increased accuracy. The investigations described above provide some support for this assumption. As far as the relative reward values are concerned, the results of the studies described in this chapter demonstrate that increasing relative values of rewards available in a task can lead to increased accuracy in certain circumstances, but that this effect is not consistent. More specifically, they show that increasing relative reward values leads to increased accuracy on physical effort trials, so the trials that seem to be relatively easy for participants (accuracy is high on these trials). At the same time, relative reward values seem to have little effect on accuracy during mental effort trials, which seem to be rather difficult for participants (accuracy on these trials is low). This pattern of results suggests either that relative reward values influence accuracy only when the effort required is physical, but not mental (‘effort type’ hypothesis), or that relative reward values have an impact on accuracy only when the task at hand is relatively easy (‘difficulty’ hypothesis).

The results of the investigations examining the effects of increasing absolute reward values on accuracy seem to support the latter hypothesis. In Experiment 4 participants were found to adjust their accuracy in line with absolute reward values on low mental effort trials and high physical effort trials, so trials of medium difficulty, judging by the accuracy achieved by participants on these two types of trials. No effects of absolute reward values were found on high mental effort trials, possibly because they were too difficult and participants could not increase their accuracy on them even if they wanted to. Furthermore, no effects of rewards were found on low physical effort trials, during which accuracy was almost 100%, so could not be improved further.

Taken together, the results of these analyses suggest that increasing relative and absolute reward values will only lead to increased accuracy on tasks of medium difficulty. On difficult tasks rewards will have little effect on accuracy, as people do not have the skills or resources necessary to increase it. On easy tasks, on the other hand, accuracy will not increase either, as people are already very accurate.

b) Effects of manipulating reward valence on accuracy

According to the V-E-D-M model changing the valence of rewards available during a task should lead to changes in the amount of effort exerted, and consequently the accuracy achieved. More specifically, accuracy should be higher when participants face potential losses, as people seem to be more risk averse in such situations. The results of the experiments described above provide partial support for this hypothesis. In Experiment 3 participants from the Loss group were found to be more accurate than participants from the Gain group on low mental effort trials, especially when these trials were associated with high losses. Nevertheless, the effects of reward valance were limited to mental effort trials only. Such result suggests that changing the reward valence in an effort-based decision-making task might affect accuracy on mental effort, but not physical effort tasks (‘effort type’ hypothesis), or that changing reward valence might affect accuracy on tasks which are difficult (‘difficulty’ hypotheses). The second hypothesis fits well with the assumption that people are more risk averse when losses are at stake, as it suggests that in the face of losses participants increase their accuracy on tasks which are difficult and therefore associated with a high probability of failure, but not on the easy tasks during which probability of failure is small anyway. Therefore, results of the investigations described in this chapter suggest that reward valence has a potential to affect effort-based decision-making, but only on difficult tasks during which the probability of failure is high.

c) Effects of manipulating reward reliability on accuracy

According to the V-E-D-M model, along with reward magnitude and reward valence, reward reliability is an important factor affecting effort-based decision-making. The model assumes that increasing reward reliability should lead to increased accuracy on tasks which require effort exertion. Results of the experiments described in this chapter provide very little support for this hypothesis, however, as most investigations looking at the effects of reward reliability presented in previous sections did not find any differences in accuracy between groups obtaining rewards on 50%, 75%, or 100% of successful trials. There was some indication in Experiment 5 that participants on high mental effort trials might be more accurate when the reward was deterministic than when it was probabilistic, but this was an isolated finding, from which it is difficult to draw any strong conclusions. In general, the results of the investigations described in this chapter do not provide strong support for the hypothesis that reward reliability affects accuracy on effort-based decision-making tasks.

2) Effort manipulations

One of the implicit assumptions of the V-E-D-M model is that mental and physical effort are processed in the same way during effort based decision-making. To investigate this assumption accuracy on mental and physical effort trials was compared in the experiments described in this chapter. The main finding of these comparisons was that participants were much more accurate on physical effort trials compared to mental effort trials. This, in turn, suggests that physical effort trials were less difficult for participants than mental effort trials, which has important consequences for the interpretation of potential differences between mental and physical effort found in the six experiments described in this thesis. It means that these differences can either be due to genuine differences in processing of mental and physical effort or due to differences in task difficulty. It also means that no strong conclusions about the differences in processing of mental and physical effort can be drawn based on the results described in this thesis.

3) Importance of effort/reward during Action Selection and Action Execution

According to the V-E-D-M model Action Execution is driven by subjective values assigned to the available options during the valuation stage. These subjective values are based on the reward values and effort requirements associated with each option. However, which one of these factors plays a more important role in determining accuracy during Action Execution is less clear. The investigations described in this chapter suggest that effort requirements are the primary factor determining accuracy on effort-based tasks, with participants being more accurate when effort required is low. However, rewards also seem to play a role in certain circumstances because participants were found to be more accurate on high reward trials compared to low reward trials when physical effort was required. These findings can be taken to suggest that rewards drive accuracy when effort required is physical, but not mental (‘effort type’ hypothesis) or that rewards mainly play a role in determining accuracy during tasks of medium difficulty (‘difficulty’ hypothesis). The latter hypothesis is in line with what has been established in the section describing the effects of manipulating reward magnitude, making the ‘difficulty’ explanation more likely.

4) Outcome feedback

Considering that outcome feedback plays an important role during Outcome Evaluation, V-E-D-M model assumes that changing the informative value of this feedback (e.g. changing the amount of information it provides about rewards) should have an effect on effort-based tasks. This hypothesis, however, has not been supported by the results of investigations described in this chapter, as no significant effects of feedback on accuracy were found. Overall, this suggests that cumulative, discreet, and simple feedback do not impact effort-based decision-making differently.

5) Delayed Action Execution

According to the V-E-D-M model, learning plays a crucial role in updating representations based on which future decisions are made. Therefore, preventing learning through delaying Action Execution and Outcome Evaluation could potentially have a big impact on the effort-based decision-making process, possibly by affecting the accuracy of performance. Results of Experiment 2 provide some support for this hypothesis because participants in the Delayed

Execution group were found to be less accurate on the low mental effort trials compared to participants who executed their actions directly after each choice. Nevertheless, no effects of delaying execution were found on physical effort trials, which suggest that the effects of delaying Action Execution on accuracy are rather limited. In line with the ‘effort type’ hypothesis, the results of this experiment suggest that delaying execution might impact accuracy when effort required is mental, but not when it is physical. Alternatively, ‘difficulty’ hypothesis suggests that delaying execution might impact accuracy on difficult tasks, but not on easy tasks. This will be discussed in more detail in Chapter 7.

6) Neural underpinnings

Neurobiological studies on which V-E-D-M model is based suggest that dopamine is crucial for invigorating action and increasing effort expenditure. Since increased effort expenditure is thought to translate into increased accuracy, it was hypothesised that impaired dopaminergic neurotransmission might have an impact on accuracy during effort-based decision-making task. However, no evidence of a relationship between dopamine and accuracy was found in Experiment 6, suggesting that dopamine might not play an important role in translating effort exertion into accuracy. At the same time the results of this study need to be treated with caution, as participants taking part in this study were on dopamine replacement therapy, which might have affected the results.

6.3 Summary

The results of the studies presented in this chapter point to the importance of investigating accuracy on effort-based decision-making tasks. It can prove very helpful in interpreting the results obtained through examining the choices people make and the amount of effort they exert during effort-based decision-making tasks. Taken together, the results from these three measures provide crucial information for establishing the validity of the assumptions of the V-E-D-M model proposed in this thesis. Therefore, in the next chapter participants’ choices, effort exertion and accuracy are examined together. Based on these examinations a revised version of the V-E-D-M model is proposed.

CHAPTER 7: General Discussion

Effort-based decision-making is a process people engage in when they have to trade off the costs and benefits of putting in effort (conventionally, though not always, seen as a cost) to gain a reward. This type of situation is subsumed into a more general form of decision-making, commonly referred to as value-based decision-making. Value-based decision-making concerns any situation in which a decision maker has to offset the gains against the costs of selecting a particular option from alternatives. During effort-based decision-making the specific cost that needs to be taken into account is effort.

People engage in effort-based decision-making on a daily basis, whenever they have to decide if it is worth putting in effort to obtain rewards. In spite of the fact that it is so widespread, the mechanisms driving this process are still relatively unknown and no formal models of effort-based decision-making exist. Therefore, in this thesis a novel model of effort-based decision-making, the V-E-D-M model, was introduced. Unlike previous models, on which it was based (by Assadi et al., 2009; Doya, 2008; Ernst & Paulus, 2005; Kable & Glimcher, 2009; Rangel et al., 2008; Rigoux & Guigon, 2012), the V-E-D-M model concentrated specifically on effort-based decision-making, rather than value-based decision-making in general.

The V-E-D-M model assumed that effort based decision-making consists of six stages: 1) **Representation**, 2) **Valuation**, 3) **Action Selection**, 4) **Action Execution**, 5) **Outcome Evaluation**, and 6) **Learning** (see Figure 1). During the **Representation** stage people encode the options available in a given decision-making scenario. This is followed by the **Valuation** stage, during which each option is assigned a subjective value, based on the benefits associated with this option and the effort required to obtain them. This subjective value constitutes the basis on which different options are then compared during the **Action Selection** stage**,** and the most beneficial option is chosen. Once an option has been selected, it is executed during the **Action Execution** stage. The feedback generated by this process is then evaluated during the **Outcome Evaluation** stage, and this serves as a basis for updating representations during the **Learning** stage.

The V-E-D-M model makes certain assumptions regarding processing of effort, rewards, and feedback during the six stages described above. Some of these assumptions overlap with the assumptions made by the existing value-based decision-making models described in Chapter

1. Many of them have never been investigated before, however, which means that there are core assumptions the V-E-D-M model makes for which there is either limited or no evidence. These assumptions relate to six specific areas: 1) Reward manipulations, 2) Effort manipulations, 3) Importance of effort/reward during Action Selection and Action Execution 4) Outcome feedback, 5) Delayed Action Execution, and 6) Neural underpinnings. For example, based on results of previous studies, the model assumes that rewards play a crucial role in determining subjective values assigned to options. These values are thought to drive Action Selection and Action Execution, and so manipulating important reward characteristics such as reward magnitude, valence and reliability should influence behaviour during these two stages. In line with previous literature, the model also makes the assumption that mental and physical effort are processed in the same way throughout the stages of decision-making. In addition, it states that feedback from the decision-making process forms the basis for Outcome Evaluation, and so manipulating reward feedback or delaying Action Execution should have an impact on Outcome Evaluation and Learning. Finally, it predicts that altered dopaminergic neurotransmission should affect effort processing, due to an important role of this neurotransmitter during effort-based decision-making.

To assess the validity of the assumptions described above, the effects of manipulating reward, effort, and feedback on effort-based decision-making were investigated in six experiments forming the empirical part of this thesis. More specifically, these six experiments examined the effects of manipulating 1) reward: a) magnitude, b) valence, c) reliability, 2) effort type, 3) effort level, 4) feedback, 5) timing of execution, and 6) dopamine on behaviour during a novel effort-based decision-making task. The rest of this chapter will survey the key results from these experiments across three critical behavioural measures (i.e. choice of action, execution of actions, and accuracy of performed actions) and relate them back to the V-E-D-M model. From this evaluation, a modified version of the V-E-D-M model will be proposed (see Figure 24). The discussion will end with some consideration of the type of experimental design used in the present project.

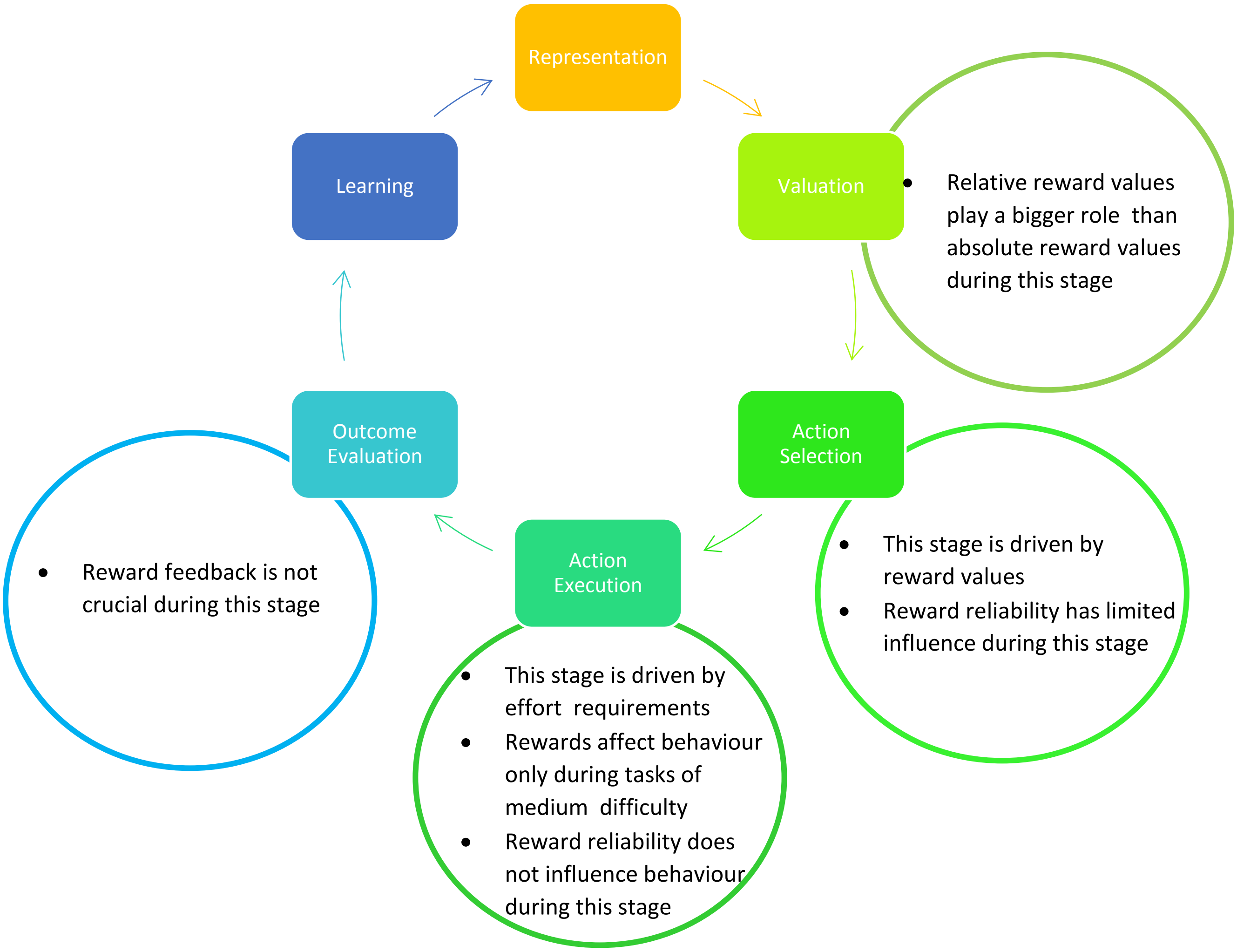


Figure 24. Modified Value-Effort Decision-Making model. Assumptions added to the model in response to the findings of this thesis are presented in circles.

7.1 Reward manipulations

7.1.1 Reward magnitude

The V-E-D-M model assumes that rewards play a crucial role during effort-based decision-making. They are supposed to affect subjective values assigned to options during the Valuation stage, determine which option gets chosen during the Action Selection stage, and influence how much effort is put in during the Action Execution stage. In general, the model assumes that increasing rewards should lead to an increase in the subjective values attached to the choice alternatives people face. This, in turn, should lead to an increased willingness to choose effortful actions, increased effort expenditure, and increased accuracy. Studies of effort-based decision-making conducted so far seem to generally support this assumption. They show a strong influence of reward on effort-based choices and execution (Bijleveld et al., 2012; Bijleveld et al., 2014; Bonnelle et al., 2014; Burke et al., 2013; Capa et al., 2011;

Chong et al., 2015; Croxson et al., 2009; Hartmann et al., 2013; Kool & Botvinick, 2014; Krebs et al., 2012; Kurniawan et al., 2013; Le Bouc & Pessiglione, 2013; Marien et al., 2014; Pas et al., 2014; Pessiglione et al., 2007; Treadway et al., 2009; Zedelius et al., 2011).

Nevertheless, the results of some investigations suggest that the relationship between rewards and effort might not be as straightforward. For example, several experiments have found that rewards modulate effort exertion when the effort that is required is high, but not when it is low (e.g. Bijleveld et al., 2009; Bijleveld et al., 2012; Bijleveld et al., 2014; Marien et al., 2014). Other experiments have observed that rewards influence how much effort is put in during tasks of medium difficulty, but not during very difficult tasks (Glucksberg, 1962; Pelham & Neter, 1995; W. F. Wright & Aboul-Ezz, 1988). Furthermore, most of the studies mentioned above have looked at relative, rather than absolute rewards. With the exception of the empirical investigations described in this thesis, there has been no work examining the effects of increasing absolute reward values on performance during effort-based decision-making. For that reason, the effects of increasing relative and absolute reward values on participants' behaviour during choice and execution were examined in the six experiments described in this thesis.

In general, the findings from these experiments suggest that the effects of rewards differ depending on the stage of the decision-making process. During the Action Selection stage increasing relative, but not absolute, reward values was found to lead to an increased willingness to choose effortful options, in line with the V-E-D-M model assumptions and previous studies (Bonnelle et al., 2014; Chong et al., 2015; Kurniawan et al., 2010; Treadway et al., 2009). During the Action Execution stage, on the other hand, the effects of increasing relative and absolute reward values were found to be limited. In three out of six experiments (Experiment 1: Gains; Experiment 3: Reliability; Experiment 4: Increased rewards) no effects of increasing relative rewards on effort expenditure were observed, as participants exerted similar amounts of effort on trials associated with high and low rewards. Participants facing potential losses (Experiment 2: Losses) were found to put in more effort when rewards were high, but this effect was observed only on low mental effort trials and high physical effort trials. Participants required to execute their choices immediately after making them (Experiment 5: Immediate Execution) were also found to exert more effort for higher rewards, but only on physical effort trials. The general conclusion from these findings seems to be that even though rewards influence the choices people make, their effect on effort expenditure is limited. More specifically, rewards seem to affect effort exertion only in certain circumstances. The investigations of participants' accuracy during the effort-based decision-making task can shed a light as to what these circumstances might be.

Analysis of the accuracy data suggests that the effect of rewards on effort exertion might be mediated by task difficulty. As mentioned in the previous paragraph, participants were found to increase their effort exertion in response to high rewards on low mental effort trials and high physical effort trials in Experiment 2, and on physical effort trials in Experiment 5. Analysis of participants' accuracy on these trials suggests that they shared a common characteristic – they were of medium difficulty. Participants were found to be significantly more accurate on these trials than on high mental effort trials in Experiments 1, 2, 5 and 6 (see Appendix B). At the same time, participants were found to be less accurate on these trials than on low physical effort trials. This pattern of findings suggests that low mental effort trials and high physical effort trials were of medium difficulty compared to the other types of trials available during the task. Considering that participants were found to increase their effort exertion in response to high rewards on these two particular types of trials in Experiments 2 and 5, it implies that relative reward values influence effort exertion only on trials of medium difficulty. Results of several previous studies provide further support for this hypothesis. For example, Glucksberg (1962) manipulated task complexity in two experiments involving a problem solving task and a perceptual task. In each experiment, incentives were found to have a positive effect on performance in the easy version of the task but a negative effect on performance in the complex version. Similarly, Pelham and Neter (1995), using judgement tasks of different levels of difficulty, observed that subjects who received the easy version of the task performed better with incentives, while those subjects who received the complex version did not. Finally, W. F. Wright and Aboul-Ezz (1988) asked business school students to perform frequency assessments for monetary rewards, and they found that incentives had a greater positive effect in simple tasks than in more complex tasks. Nevertheless, the hypothesis that rewards influence effort exertion only on tasks of medium difficulty does not account for all the findings presented above. For example it does not explain why rewards should only affect performance when losses are at stake or the execution is immediate (Experiments 2 and 5), or why should they affect effort-based choice and execution differently.

All in all, the findings from the six studies described in this thesis suggest that the relationship between rewards and effort during effort-based decision-making is not as straightforward as assumed by the V-E-D-M model. First of all, it seems that the effects of rewards depend on the stage of decision-making people are involved in. During the Action Selection stage increasing relative (but not absolute) reward values increases people's willingness to choose effortful options, which is consistent with the model and prior research. However, rewards *per se* have a limited effect on execution, and this appears to be mostly in specific contexts (e.g. when losses are at stake or execution of an action is immediate), and only on tasks of medium difficulty. Second, evidence presented in this thesis suggests that increasing absolute rewards does not impact on behaviour during effort-based decision-making. It does not influence choices people make during Action Selection, and it has limited consequences for performance during Action Execution.

Modified model

In response to the results presented above, the V-E-D-M model was modified (see Figure 24). In the revised V-E-D-M model relative reward values are assumed to affect behaviour more than absolute reward values during effort-based decision-making. Furthermore, the effects of rewards on effort processing are assumed to depend on the stage of the decision-making process. Relative rewards are thought to affect the willingness to choose effortful options during the Action Selection stage. At the same time, they are assumed to have a limited impact on effort exertion during the Action Execution stage. During this latter stage, influence of rewards is assumed to be limited to tasks of medium difficulty. These modifications to the model raise three important questions: 1) Why should relative reward values matter more than absolute reward values when making effort-based decisions? 2) Why should rewards affect behaviour differently at different stages of decision-making? 3) Why should rewards influence behaviour on trials of medium difficulty, but not on easy or difficult trials? The following section suggests potential answers to these questions, providing a rationale for the modifications to the V-E-D-M model and explaining some of the findings presented in this thesis.

The first assumption of the modified V-E-D-M model is that relative reward values matter more than absolute reward values when making effort-based decisions. The Decision by Sampling (DbS) model (Stewart, Chater, & Brown, 2006) provides a plausible explanation as to why this might be the case. This model suggests that there is no such thing as an innate value weighting function or scale representing absolute reward values within the decision-making process. Rather, the value of rewards experienced within a decision-making scenario is construed based on previous experiences stored in memory. Choice between different options is made based on a rank ordering system which compares the attributes of different options with similar items recalled from memory. Several neuroimaging studies provide support for the DbS model, showing context-dependent activations in response to different monetary values in ventral striatum, vmPFC and ACC (Elliott, Newman, Longe, & Deakin, 2003; Mullett & Tunney, 2013). The implication of this model is that manipulating relative reward values within a task should have a bigger impact on performance than manipulating absolute reward values between tasks (especially when the differences between rewards available in these tasks are not big). This is because the relative reward values experienced at the beginning of a task provide a fresh trace in memory to which all the other values within a task can be compared. Nevertheless, this hypothesis requires further investigations. These investigations could introduce additional information into the task set-up, aimed at altering the recent memory traces associated with rewards. From the work in this thesis, the prediction that follows is that changing recent memory traces associated with rewards should affect the values attached to different options, leading to changes in behaviour during Action Selection and Action Execution.

Another assumption the revised V-E-D-M model makes is that rewards should affect behaviour during the Action Selection stage, but not during the Action Execution stage. This might be because people shift their attention from rewards to effort requirements once they begin to exert effort. For example, Hutchinson and Tenenbaum (2007) monitored a group of participants during two effortful tasks: a hand grip task and a stationary cycling task. They asked participants to verbally report all the thoughts they had while exerting effort. Hutchinson and Tenenbaum (2007) found that as the effort requirement increased, so did the number of thoughts related to the physical sensation of effort reported by participants. Tenenbaum and Connolly (2008) observed similar effects in a group of university rowers asked to row at 30%, 50%, or 75% of their maximum capacity. They have found that rowers had a tendency to concentrate on the bodily sensations associated with effort exertion during the task, and even more so as the effort requirements increased. Overall, this set of findings suggests that during effort exertion people tend to focus on the effort component of the task, especially when the effort required is high.

In line with these findings, Boksem and Tops (2008) suggested that effort exerted during mental and physical effort tasks is constantly monitored during the Action Execution stage. The purpose of this monitoring is to determine if an effortful action should continue or should be abandoned. They claim that the effort already expended is taken into account in an ‘online’ cost/benefit analysis that goes on during Action Execution. If the effort expended is perceived as exceeding the value of potential reward, then this results in decreased motivation and increased fatigue, or even cessation of effortful behaviour altogether. By extension, Meyniel et al. (2014) proposed the existence of a *cost evidence signal* which accumulates during Action Execution, which influences the level of motivation invested in carrying out an effortful task.

Furthermore, Gilbert and Fiez (2004) and Pochon et al. (2002) demonstrated that activation in the ventral frontal cortex (VFC), responsible for reward processing, increased in response to rewards presented in preparation for a cognitively demanding task. At the same time, activation in this structure decreased substantially during the execution of the task. Pochon et al. (2002) concluded that VFC activity might be suppressed during cognitively demanding tasks in order to minimize interference by thoughts and emotional responses evoked by a reward.

Taken together, the evidence presented above suggests that different effects of rewards during Action Selection and Action Execution might stem from the fact that the relative importance of these two factors changes from the former stage to the latter. It seems that during Action Selection rewards determine subjective values of options, and so are more likely to influence behaviour. During Action Execution, on the other hand, effort becomes more salient than reward, and so rewards do not affect behaviour as much. To lend further support to this interpretation, future studies could utilise other, more reliable techniques of investigating the focus of participants during Action Selection and Action Execution, for example eye tracking. Based on the results described in this thesis, the prediction would be that participants should focus their attention on cues associated with rewards during the Action Selection stage, and on cues associated with effort during the Action Execution stage.

Finally, the revised V-E-D-M model assumes that during Action Execution rewards should mainly influence effort exertion on tasks of medium difficulty. The simplest explanation as to why this might be the case is that on such tasks increased effort exertion translates into increased chances of obtaining a reward. This is not always the case on the very easy or very difficult tasks. On easy tasks, during which accuracy is very high anyway, additional effort exertion cannot improve performance due to the ceiling effect, and so there is no point putting in extra effort. On difficult trials, on the other hand, participants may not have the skills necessary for improving performance, and so additional effort exertion may not translate into higher chances of obtaining rewards. On tasks of medium difficulty, however, participants should have the skills necessary to improve performance and increase accuracy, and so it is worth for them to increase their effort exertion when rewards are high, to increase their chances of obtaining them. This explanation is in line with the findings of Camerer and Hogarth (1999), who conducted a review of 74 studies investigating the effects of monetary incentives on performance. From this review, they have concluded that monetary rewards are capable of improving task outcomes, but only when increasing effort expenditure improves performance. On tasks in which there is intrinsic motivation to perform well, or additional effort does not matter because the task is too difficult or has an upper payoff limit which can be easily reached, rewards do not affect behaviour. This conclusion has been supported by Bonner et al. (2000) reading of the finance and management literature. They also found that as task difficulty increased, the influence of rewards of performance decreased. Nevertheless, considering that investigating the effects of rewards on performance during tasks of different difficulty was not one of the explicit aims of this thesis, this area requires further investigations. Specifically, further studies looking at the effect reward magnitude on easy, medium, and difficult tasks are needed, to establish if the effect of reward on effort exertion is mediated by the task difficulty. From the empirical work in this thesis, the prediction would be that in such studies the effects of rewards should be observed solely on the task of medium difficulty.

7.1.2 Reward valence

Besides reward magnitude, another factor which is assumed by the V-E-D-M model to affect effort-based decision-making is reward valence. More specifically, the model assumes, in line with studies on risk-based decision-making by Kahneman and Tversky (1979), that people are risk averse in the face of losses. This risk aversion should translate into reduced preference for effortful options during Action Selection, as well as increased effort expenditure and increased accuracy during Action Execution. However, evidence exists to suggest that this might not always be the case. For example, Kurniawan et al. (2013), conducted an experiment which involved squeezing a hand grip to win or avoid losing money. In this experiment they observed shorter reaction times and faster speed to reach the grip strength required when participants had a chance to win money as opposed to losing it. This means that participants were exerting more effort in the face of gains rather than losses, which suggests that they were not risk averse. Ambiguous results such as this from the limited work on the effect of reward valence on effort-based decision-making were a key reason for exploring this further in this thesis.

The evidence from the studies presented in the previous chapters generally supports the assumption of the V-E-D-M model that people become risk-averse in the face of losses and that this affects effort-based decision-making. As far as the Action Selection stage is concerned, the present work showed that participants making effort-based decisions with the aim of avoiding losses were more likely to choose easy, low effort options compared to participants aiming to obtain gains. This suggests that participants in the Loss group had a preference for options associated with a lower risk of failure during this task, which fits with the assumption that people are risk averse when losses are at stake.

Furthermore, during Action Execution participants facing losses were found to exert more effort than participants facing gains, although this effect was limited to mental effort trials. Considering that mental effort trials were more difficult for participants, and therefore associated with a higher risk of failure and incurring a loss, this result also fits with the assumption that people are risk averse. Moreover, it suggests that the increase in effort exertion in response to losses depends on how risky/difficult the task is, with participants increasing their effort expenditure on tasks which are risky/difficult, but not on tasks which are relatively risk-free/easy.

The results of the investigations into the effects of gains and losses on accuracy also support this interpretation. They showed that, compared to participants facing gains, participants facing losses were more accurate on difficult, mental effort trials, but not on easy, physical effort trials. Participants were also found to be more accurate on mental effort trials associated with high potential losses compared to trials associated with low potential losses, further suggesting that participants were particularly risk averse when the consequences of failure were most severe.

All in all, the results of the studies described in this thesis confirm the assumption of the V-E-D-M model that people are risk averse in the face of losses and that they adjust effort-based decision making process to minimize the risk of failure when losses are at stake.

The results presented above are well explained by the principle of loss aversion, as proposed by Kahneman and Tversky (1979). In Prospect Theory (1979), they suggested that people assess potential outcomes of a decision-making scenario in relation to a reference state, and that during this assessment potential losses loom larger than gains (see also Tversky & Kahneman, 1991), which leads to increased risk aversion in response to losses. Our findings demonstrate how this risk aversion plays out during effort based decision-making tasks, showing that it leads to avoidance of options associated with high effort during Action Selection and increased effort exertion during Action Execution.

However, an alternative explanation of our findings is provided by the psychological law of inertia, as proposed by Gal (2006) and Kahneman (2011). Psychological law of inertia states that people have a propensity to remain at the status quo, which determines their behaviour when gains and losses are at stake. In the case of the Loss experiment described in this thesis, the law predicts that participants should behave in a manner that would reduce the chances of a change in the status quo, so a change in the initial endowment of £6.40. The findings of this thesis support this prediction, showing that people engaged in behaviours aimed at preventing change in the sum of money given to them at the beginning of experiment. They did it through choosing low effort options during Action Selection and exerting more effort during Action Execution.

Considering that both loss aversion (Kahneman & Tversky, 1979) and psychological law of inertia (Gal, 2006; Kahneman, 2011) explain the pattern of findings presented in this thesis, further investigations are needed to establish which one of these principles drives behaviour during effort-based decision-making tasks. If maintaining the status quo is important, it can be predicted that in future tasks people should not alter their behaviour in response to losses, providing that these losses do not affect the endowment guaranteed at the beginning of the task. If, however, people are loss averse, changes of behaviour in response to losses would be expected, regardless of whether the losses diminish the initial endowment or not.

7.1.3 Reward reliability

In addition to magnitude and valence, another important reward characteristic thought to affect effort-based decision-making according to the V-E-D-M model is reliability. More specifically, the model assumes that the willingness to choose and perform effortful actions should increase in line with the probability of obtaining rewards, and so people should be most willing to invest effort when rewards are guaranteed. Results of the studies using probabilistic rewards as incentives during effort-based decision-making tasks provide some support for this hypothesis. They show that people are more willing to choose effortful options (Treadway et al., 2009), more willing to exert effort, and more accurate (Kurniawan et al., 2013) when probability of obtaining rewards is high. However, in the absence of a larger number of studies investigating the effects of reward reliability on effort based decision-making, it is impossible to assess the validity of the assumption made by the V-E-D-M regarding the effects of probabilistic rewards. Therefore, one of the aims of this thesis was to investigate the effects of reward reliability on Action Selection and Action Execution, to provide evidence clarifying this issue.

In general, results of the investigation conducted in this thesis suggest that the relationship between reward reliability and effort is not as straightforward as assumed by the V-E-D-M model. Contrary to the predictions of the model, no effects of changing the probability of obtaining rewards on effort exertion and accuracy during the Action Execution stage were observed. During the Action Selection stage, participants were found to behave in a similar way when rewards were deterministic and when they were unreliable. In both conditions participants showed a strong preference for low effort trials over high effort trials. In contrast, participants experiencing probabilistic rewards were found to be just as likely to choose high effort trials and low effort trials. They were also found to be more likely to choose high effort trials than participants experiencing deterministic rewards.

The fact that participants in the probabilistic condition were found to be just as likely to choose high and low effort trials is somewhat surprising considering the assumptions of the V-E-D-M model and the results of the previous studies. One of the possible explanations of this finding is that participants in the probabilistic condition made an implicit association between effort exertion and acquisition of rewards, and consequently increased their choices of high effort trials in an attempt to maximize gains. Since in the probabilistic condition rewards could be obtained on 75% of successful trials, increased effort exertion did indeed maximize the probability of obtaining rewards in this condition. It seems likely that participants generalized from this observation made during the Training phase to the Choice phase, and assumed that increased willingness to exert effort should also translate into higher probability of obtaining rewards, which would explain their pattern of choices. However, further studies would be required to confirm if this was actually the case. These studies should investigate if changing participants' beliefs regarding the effects of increased effort expenditure on the probability of obtaining rewards would have an impact on behaviour during Action Selection.

Taken together, the results described above indicate that the effects of reward reliability on effort-based decision-making depend on the stage of this process. During the Action Selection stage, altering reward reliability seems to have no effect on the choices people make, unless it leads people to believe that by increasing their effort expenditure they can increase their chances of obtaining rewards. During the Action Execution stage, reward reliability seems not to affect behaviour at all.

Modified model

In response to these findings, the V-E-D-M model was modified (see Figure 24). The revised version of the model assumes that the effects of reward reliability differ depending on the stage of effort based decision-making. During Action Selection, reward reliability has a potential to influence behaviour, but only if a decision-maker believes that their choices can influence the likelihood of obtaining rewards. During Action Execution, reward reliability does not affect performance. These modifications to the model raise an important question: Why should reward probability affect Action Selection stage, but not Action Execution stage?

A possible explanation is that rewards are more salient during Action Selection than during Action Execution. As described in section 7.1.1, evidence exists to suggest that during Action Execution people tend to concentrate on the effort requirements of a task, rather than on rewards (Boksem, Meijman, & Lorist, 2006; Gilbert & Fiez, 2004; Hutchinson & Tenenbaum, 2007; Meyniel et al., 2013; Pochon et al., 2002; Tenenbaum & Connolly, 2008). It is, therefore, possible that during this stage people pay less attention to different reward characteristics, and this is why no effects of reward reliability on effort exertion were found in this thesis. One test of this would be to assess the focus of attention during Action Selection and Action Execution using methods such as eye tracking, as described in section 7.1.1. This would help to establish which components of the decision-making scenario are attended to during effort-based choice and execution.

7.2 Effort manipulations

In addition to the hypotheses regarding the effects of different reward characteristics on effort-based decision-making, V-E-D-M model also makes assumptions about the effects of effort type. More specifically, the model assumes that mental and physical effort are processed in a similar way and so their effects on effort-based decision-making should be comparable. This assumption is supported by the results of several studies investigating effort exertion during mental and physical tasks, showing similar pattern of results for these two types of effort (e.g. Ostaszewski et al., 2013; Pas et al., 2014). Nevertheless, direct comparisons of effort-based decision-making during mental and physical tasks are rare, and so one of the aims of this thesis was to investigate the potential similarities and differences in processing of mental and physical effort during effort-based decision-making.

Contrary to the assumption of the V-E-D-M model that mental and physical effort are processed in the same way during effort-based decision-making, differences in behaviour on mental and physical effort trials were observed in this thesis. However, the interpretation of this finding is problematic, considering that mental effort trials were found to be more difficult for participants than physical effort trials, based on the accuracy achieved by participants across experiments. This, in turn, means that the differences between mental and physical effort identified in this thesis might either reflect 1) genuine differences in processing of mental and physical effort, or 2) differences in task difficulty.

The latter of the two explanations seems particularly likely, considering that task difficulty has been found to affect behaviour in previous studies investigating the effects of monetary rewards on performance. For example, Bailey and Fessler (2011) asked participants to complete jigsaw puzzles of different levels of difficulty for an opportunity to win small monetary rewards. They found that monetary rewards improved participants' performance on tasks of low difficulty, but had little effect on performance during difficult tasks. Furthermore, R. A. Wright, Contrada, and Patane (1986) examined cardiovascular reactivity (as a measure of effort exertion) in response to monetary incentives during memory tasks of different difficulty (low vs. medium vs. high). They observed that monetary incentives had an impact on cardiovascular responses, and therefore on effort exertion, during tasks of medium difficulty but not easy or very difficult tasks.

Bonner and Sprinkle (2002), based on a review of available literature, suggested that task difficulty can 1) decrease effort intensity and effort duration during a task, leading to decreased performance, and 2) attenuate the effects of effort on performance through increasing skill requirements. Decrease in effort intensity and duration is observed when rewards available are not deemed worth the increased effort expenditure necessary to complete the task. Attenuation of the effects of increased effort exertion, on the other hand, is observed when rewards are deemed worth the effort required, but participants lack the skills necessary for successful completion of the task. General conclusion from the review by Bonner and Sprinkle (2002) was that increased task difficulty is likely to attenuate positive effects incentives have on effort exertion. The results presented in this thesis seem to support this conclusion, as participants were found to modulate their performance in response to rewards on physical effort trials, which were relatively easy, but not on mental effort trials, which were difficult.

Considering the results of the previous studies presented above, it is likely that the differences in behaviour between mental and physical effort trials observed in this thesis result from the differences in task difficulty, rather than genuine differences in processing of these two types of effort. For that reason, the investigations described in this work do not provide the necessary information needed to establish the validity of the assumption of the V-E-D-M model that mental and physical effort are processed in a similar way. Therefore, further investigations are required. Development of mental and physical effort tasks of similar difficulty, as measured by participants' accuracy, would be of paramount importance for these investigations. Furthermore, including trials of various difficulties (e.g. low vs. medium vs. high) would also be essential. In such a task set-up, participants should show no differences in behaviour on mental and physical effort tasks of similar difficulty, providing that mental and physical effort are processed in a similar way. Furthermore, if task complexity influences performance during mental and physical effort trials, as hypothesised above, differences in behaviour on tasks of different difficulty should be observed.

7.3 Importance of effort/reward during Action Selection and Action Execution

One of the main assumptions of the V-E-D-M model is that Action Selection and Action Execution are driven by subjective values assigned to available options during the valuation stage. These subjective values are thought to be based on the reward values associated with each option and the estimated effort required for obtaining them. However, which one of these factors is more important in driving behaviour during effort-based decision-making is yet to be established. Many studies conducted so far suggest that rewards are the main determinant of choice and execution. They show that participants consistently select options associated with higher rewards and exert more effort on high reward trials during effort-based decision-making tasks (e.g. Bijleveld et al., 2009; Bijleveld et al., 2010, 2011, 2012; Bijleveld et al., 2014; Bonnelle et al., 2014; Hartmann et al., 2013; Kool et al., 2010; Krebs et al., 2012; Le Bouc & Pessiglione, 2013; Marien et al., 2014; Pas et al., 2014; Pessiglione et al., 2007; Treadway et al., 2009; Zedelius et al., 2011). However, other studies suggest that monetary rewards are not necessary for effort mobilization (e.g. Botvinick et al., 2009; Kroemer et al., 2014; Satterthwaite et al., 2012). In fact, Brehm and Self (1989) suggest that during Action Execution effort invested in a task depends not on the incentives present, but rather on the task difficulty. In their Theory of Motivation, Brehm and Self (1989) postulate that rewards determine *potential motivation*, defined as the maximum level of effort people are willing to exert to obtain these rewards. As long as effort required by the task falls within the limit set by potential motivation, the actual level of effort exerted during the task should depend on task difficulty rather than reward values. Therefore, two competing views exist as to what drives effort-based choice and execution: reward values or effort requirements. The validity of these competing views was examined in the six experiments forming the empirical part of this thesis.

The main finding of these investigations is that that different factors seem to play a role during the Action Selection stage and the Action Execution stage. During Action Selection rewards seem to be the most important aspect taken into account when making choices, as participants were consistently found to select trials associated with high rewards throughout the six experiments described in this thesis. During Action Execution, on the other hand, the amount of effort required to obtain rewards was found to be a more consistent predictor of behaviour, with participants exerting more effort on high effort trials compared to low effort trials regardless of the rewards associated with them. Also, both effort requirements and reward values were found to influence accuracy, although the effect of rewards was only visible on tasks of medium difficulty.

Taken together these results suggest that both effort requirements and reward values drive behaviour during effort-based decision-making, but their importance changes depending on the stage of the process. Choice seems to be primarily driven by reward values, whereas effort exertion seems to be driven by effort requirements, in line with the Theory of Motivation by Brehm and Self (1989). Accuracy seems to be affected by both these factors.

Results of several studies conducted so far seem to support these conclusions. As far as the Action Selection stage is concerned, studies looking at choices people make when effort is required have consistently found a strong preference for options associated with high rewards, regardless of the effort level associated with them (e.g. Kurniawan et al., 2010; Treadway et al., 2012; Treadway et al., 2009; Wardle et al., 2012; Wardle et al., 2011). For example, Treadway et al. (2009) used a novel Effort Expenditure for Rewards Task (EEfRT) to investigate effort-based decision-making in people with different levels of anhedonia trait. This task required participants to choose between options associated with different levels of physical effort (squeezing a joystick) and reward. They found that reward magnitude was a significant predictor of people's choices, regardless of the anhedonia levels, and that participants were more willing to choose high effort trials when reward at stake was higher. Furthermore, in several other studies an increased willingness to choose effortful options was observed when rewards were increased (e.g. Bonnelle et al., 2014; Hartmann et al., 2013; Ostaszewski et al., 2013). Bonnelle et al. (2014) investigated people's willingness to exert physical effort (squeeze a joystick) for monetary rewards using an adaptive algorithm in which a choice given to a participant on a given trial depended on their previous choices. They demonstrated that people's willingness to choose effortful options in their task increased with increasing reward magnitude. Taken together, results of the studies described above suggest that choices people make during effort-based decision-making tasks are driven by reward values, in line with the findings of this thesis.

At the same time, some brain imaging studies suggest that the role of rewards becomes much less pronounced during the Action Execution stage. For example, several studies showed increased activation in the VFC (involved in reward processing) at the time of reward presentation but not during effort exertion (Gilbert & Fiez, 2004; Pochon et al., 2002). This is in line with the findings of this thesis, which suggest that during Action Execution effort exertion is driven by task requirements, rather than reward values.

Studies investigating Theory of Motivation by Brehm and Self (1989) provide further support for the claim that effort requirements drive Action Execution. For example, Eubanks et al. (2002) examined the effects of rewards on mental effort exertion during tasks of different levels of difficulty. They observed that effort exerted during a task was proportional to task difficulty, rather than incentive value. They took these results to suggest that effort expenditure during a task is normally driven by task requirements, unless effort required is so high that it can only be justified by high rewards (see also Gendolla & Richter, 2006; Marien et al., 2014; Meyniel et al., 2014).

Modified Model

Based on the evidence presented in this thesis regarding the effects of effort and reward on Action Selection and Action Execution, the assumptions of the V-E-D-M model were modified (see Figure 24). The revised model assumes that during effort-based decision-making Action Selection is driven primarily by reward values, whereas Action Execution is driven by effort requirements. At the same time, reward values can affect performance during Action Execution (particularly accuracy) providing that decision-maker has the skills necessary to complete the task (i.e. the task is not too difficult) and the amount of effort required by the task is justified by high, but not low rewards.

7.4 Outcome feedback

Another assumption that V-E-D-M model makes is that outcome feedback serves as a basis for Outcome Evaluation and Learning. For that reason altering the amount of information provided by outcome feedback can potentially have a strong impact on the effort-based decision-making process. However, this assumption has never been tested directly, despite the fact that evidence exists to suggest that cumulative, discreet and simple feedback might be processed differently during decision-making (e.g. Osman, 2011). Therefore, in this thesis the effects of these three types of feedback on effort-based decision-making were investigated.

In general, results of the studies presented in this thesis suggest that changing the amount of reward information provided by the outcome feedback does not affect behaviour during effort-based decision-making. It seems that cumulative reward feedback, or indeed any reward feedback presented after the choices are made and effort is executed, has little effect on behaviour during effort-based decision making.

Modified model

Based on the findings presented above, the V-E-D-M model was modified (see Figure 24). In the revised version of the model the amount of information about rewards that is available at the Outcome Evaluation stage is assumed not to affect effort-based decision-making to a great extent. Nevertheless, considering that V-E-D-M model stipulates that what happens during Outcome Evaluation and Learning can have important consequences for future decisions, the question remains: why no effect of different types of feedback was observed in this thesis?

The answer might lay in the structure of the task used. As described in section 3.2, during the Execution phase of the task participants were presented with the value of the potential reward each time they saw the thermometer appearing on the screen. Reward value was presented at the top of the thermometer and remained there for the duration of the trial. Once the trial was finished, participants received feedback, which could inform them about the amount of reward they obtained during the previous trial (depending on the feedback condition they were in). Nevertheless, it is likely that participants did not need such a reminder, as the reward values were fresh in their memory anyway. If that was the case, then reward feedback would provide very little additional information for participants, and so would have no effect on performance, as observed in the experiments presented in this thesis. Consequently, future investigations of the effects of reward feedback on effort-based decision-making are needed. In these future experiments reward information should be removed from individual trials, to increase the importance of feedback for outcome processing.

7.5 Delayed Action Execution

According to the V-E-D-M model, another factor that can affect Outcome Evaluation and Learning is the timing of the Action Execution stage, i.e. whether it takes place directly after the choice is made or whether it is delayed in time. Since Outcome Evaluation and Learning can only take place after action is executed, delaying Action Execution can potentially have a strong impact on effort-based decision-making. In fact, previous studies suggest that delayed execution might lead to underweighting of effort requirements at the time of choice and therefore increased preferences for effortful trials during Action Selection (e.g. Soman, 1998). One of the aims of the present work was to investigate if this pattern of results could be replicated using the novel effort-based decision-making task developed for this thesis.

In contrast to what has been found in the previous studies (e.g. Soman, 1998), the results of the present investigations suggest that delaying Action Execution can affect behaviour during effort-based decision-making, but only during the Action Execution stage. The exact effects of delaying Action Execution on behaviour during this stage were found to differ depending on the type of effort required. On mental effort trials, participants were found to exert more effort when execution was immediate. On physical effort trials participants exerted more effort when execution was delayed.

Because of the differences in difficulty between mental and physical effort trials, as described in section 7.2, interpretation of these results is difficult. It is possible that delaying Action Execution affects mental and physical effort differently. However, it is also possible that delaying Action Execution increases effort exertion during relatively easy physical tasks, but decreases it during difficult mental tasks. If the latter is the case, it would suggest that Outcome Evaluation and Learning play a more important role for effort processing when the task is difficult. It is possible that in such circumstances the opportunity to evaluate the outcome of decisions allows people to fine tune their effort exertion to the task requirements and improve their performance. During easy tasks, on the other hand, delaying effort exertion seems to be beneficial, possibly because it reduces the need to process information from trial to trial and allows people to concentrate on the task at hand.

Taken together, results presented above suggest, in line with the assumptions of the V-E-D-M model, that delaying Action Execution does influence effort-based decision-making to some extent. However, in contrast to the previous studies, it seems that the effect of this manipulation is limited to the Action Execution stage. The findings of this thesis suggest that delayed execution can lead both to increased and decreased effort expenditure, depending on the type of task. More specifically, delayed execution seems to decrease effort exertion on difficult/mental effort tasks and increase effort exertion on easy/physical effort tasks. Due to methodological issues, establishing whether it is the task difficulty or the type of effort required that modulates the effects of delaying Action Execution is impossible. Nevertheless, it seems likely that delayed execution primarily affects performance on difficult tasks. During these tasks an opportunity to fine tune effort exertion to effort requirements through Outcome Evaluation and Learning can significantly improve performance. Since this is just a speculation, however, further investigations are needed to support this hypothesis. These investigations would require manipulating task complexity, as well as the timing of the

Execution phase, to obtain the full picture regarding the effects of task difficulty on performance when execution is delayed and when it is immediate. Based on the results of the studies presented in this thesis the prediction would be that participants should perform better on difficult tasks when effort execution is immediate.

7.6 Neural underpinnings

The final aspect of effort-based decision-making investigated in this thesis was the neural basis of the mechanisms involved in this process. Based on the results of the previous studies, the examinations in this thesis focused on the neurotransmitter dopamine. This is because this neurotransmitter has been found to modulate effort processing during 1) Representation (e.g. Brooks & Berns, 2013; Phillips et al., 2007; Salamone & Correa, 2012), 2) Valuation (e.g. Prevost et al., 2010), 3) Action Selection (e.g. Chong et al., 2015), 4) Action Execution (e.g. Berridge & Robinson, 1998; Kurniawan et al., 2013; Niv, 2007; Pasquereau & Turner, 2013; Salamone & Correa, 2002; Salamone et al., 2007), and 5) Outcome Evaluation and Learning (e.g. Kable & Glimcher, 2009; Schultz, 1998, 2000, 2002, 2006, 2007, 2010; Schultz et al., 1993; Schultz et al., 1997; Schultz & Dickinson, 2000). Among other things, dopamine has been found to be crucial for overcoming effort costs and selecting effortful actions (e.g. Chong et al., 2015), as well as invigorating movements leading to the acquisition of rewards (e.g. Negrotti et al., 2005; Porat et al., 2014). For this reason, it was hypothesised that decreased levels of dopamine associated with PD should lead to decreased willingness to choose effortful options during the Action Selection stage, and decreased effort expenditure during the Action Execution stage in that group.

However, despite of the results of the previous studies suggesting that dopamine is crucial for effort-based decision-making, no differences between the dopamine-depleted PD group and HC group were observed in this thesis. PD patients were found to make similar choices, exert similar amounts of effort, and be as accurate as HCs, which suggests that dopamine might not be as important for effort processing as assumed by the V-E-D-M model. This finding is in line with the results of a previous study by MacDonald et al. (2014). In this study the role of dorsal striatum during mental effort exertion was investigated in a group of PD patients ON and OFF dopaminergic medication and HCs. To elicit mental effort exertion a symbolic distance task was used, during which participants had to make magnitude judgements regarding two numbers presented simultaneously. On effortful trials the distance in magnitude between these numbers was small, whereas on easy trials this distance was relatively big. In general PD patients were found to perform just as well on this task as HCs, regardless of whether they were tested ON or OFF medication, and no significant differences in behaviour between the two groups were found.

Furthermore, Schmidt et al. (2008) investigated physical effort exertion in PD patients and HCs. They observed that when effort requirements during a handgrip task were externally defined (i.e. given to participants at the beginning of each trial), PD patients squeezed as hard as HCs. A difference between the two groups was only observed when participants could choose how much effort to invest for monetary rewards. In such circumstances PD patients were found to exert less effort than HCs. Considering that during the effort-based decision-making tasks used in this thesis effort-based choice and execution were separated, and so by the time it came to effort exertion the amount of effort required was set and could not be changed, this might explain why no differences in effort exertion between PDs and HCs were observed in this task.

Nevertheless, overwhelming evidence from other studies investigating effort-based decision-making in PD suggests that dopamine depletion does in fact alter behaviour on effort-based decision-making tasks (e.g. Chong et al., 2015; Gepshtein et al., 2014; Jokinen et al., 2013; Majsak et al., 1998; Mazzoni et al., 2007; Moisello et al., 2011; Schneider, 2007; Weingartner et al., 1984). In light of this evidence, it seems more likely that the lack of differences between PD patients and HCs observed in this thesis stemmed from the fact that PD patients were tested ON medication. This hypothesis is supported by the results of several studies showing that performance of PD patients during effort-based decision-making tasks differs depending on whether they are tested ON or OFF medication (e.g. Anzak et al., 2012; Chong et al., 2015; Kojovic et al., 2014; Montgomery & Nuessen, 1990; Negrotti et al., 2005; Porat et al., 2014). For example, Porat et al. (2014), in their experiment investigating willingness to exert effort (through repeated finger-tapping on a keyboard) in PD patients ON and OFF medication and HCs, observed reduced effort exertion when PD patients were tested OFF medication, but not when they were tested ON medication. Furthermore, when Montgomery and Nuessen (1990) tested PD patients ON and OFF medication on a motor task which required fast reaching hand movements, they found that PD patients OFF medication had longer movement times than HCs, but this deficit was alleviated when patients were tested ON medication.

Considering the findings described above, the lack of differences between PD patients and HCs observed in this thesis is difficult to interpret without additional examination of participants' performance OFF medication. Therefore, to establish the role of dopamine during different stages of effort-based decision-making further investigations are needed. In these investigations performance of PD patients ON and OFF medication should be compared with performance of HCs, to gain a better understanding of the role dopaminergic medication plays in alleviating potential deficits in effort processing caused by PD. Furthermore, investigations of dopaminergic transmission in healthy younger adults using brain imaging techniques would also be beneficial for establishing the role of dopamine during effort-based decision-making. Such investigations could use experimental paradigm similar to the one developed for this thesis.

7.7 Limitations

As demonstrated above, studies described in this thesis provide important clarifications regarding processing of effort, rewards, and feedback during effort-based decision-making. Results of these studies have served as a basis for modifying the V-E-D-M model. They have also provided evidence that the novel task developed for this thesis can be successfully used to investigate different aspects of effort-based decision-making. Nevertheless, three methodological limitations of the task design need to be taken into account when interpreting the results.

First of all, the methods used to elicit effort exertion in this thesis were chosen from a set of tasks commonly used to examine effort-based decision-making in previous studies. This was done to allow for a direct comparison between the results of studies presented in this work and previous experiments. It is not clear, however, whether performance on these tasks can predict the general pattern of effort expenditure in real life mental and physical tasks. So far no formal comparisons between performance during laboratory-based effortful tasks and real life tasks were conducted. This is mainly because it is difficult to find appropriate, real life equivalents of the tasks used in the laboratory settings. This problem affects particularly examinations of mental effort, which use very simple, although cognitively demanding tasks, such as mental arithmetic. These tasks are rarely experienced as standalone problems in everyday lives. More commonly, they form part of more complex scenarios (such as household budgeting for example), which in turn are rarely examined in a laboratory. Therefore, the ecological validity of the findings of this thesis, as well as the previous studies requires further investigations. These investigations should focus on examining the link between lab-based task performance and effort exertion during everyday tasks which are commonly assumed to require effort.

Secondly, in the studies described in this thesis, response times, grip strength and accuracy were chosen as measures of effort exertion. However, it is not clear if these methods accurately reflect effort put in during a task. This problem also affects other paradigms used to study effort-based decision-making. In most experiments, effort exerted during a task is usually examined using task performance measures (such as response times, grip strength, or accuracy), self-report measures (such as questionnaires), or physiological measures (such as cardiovascular reactivity). These measures are assumed to be associated with effort expenditure, however, little evidence that they actually are is available. Furthermore, even assuming that the methods currently used to measure effort reflect effort exertion, few attempts to cross-validate them have been made. Self-report measures of effort expenditure are rarely used to connect task performance with participants' subjective experience of effort. The same can be said about cardiovascular measures. Even though the few studies that did combine different measures of effort exertion suggest that they are correlated to some extent (e.g. Haji, Rojas, Childs, Ribaupierre, & Dubrowski, 2015; Von Helversen, Gendolla, Winkielman, & Schmidt, 2008), further investigations of the validity of these measures are needed. The first step would be to combine different types of measurements (i.e. task performance, self-report, and cardiovascular reactivity), to explore potential relationships between them.

The final limitation of the task design used in this thesis relates to the effort requirements presented to participants. It is generally assumed that perceptions of effort vary greatly between individuals – i.e. the same task might be considered effortful by some people but easy by other people (e.g. Cocker, Hosking, Benoit, & Winstanley, 2012; Kool et al., 2010; McGuire & Botvinick, 2010; Westbrook et al., 2013). For that reason, in most of the tasks examining physical effort exertion effort requirements are adjusted for each participant. This is done through establishing participants' maximum performance level (e.g. maximum grip strength), and adjusting the effort requirements in accordance with this level (e.g. to 30%, 50%, or 75% of the maximum grip strength). This could not be done in the experiments presented in this thesis due to equipment limitations. For that reason, it is possible that the effort requirements of the tasks used were perceived differently by different participants, which could in turn affect their choices, effort exertion and accuracy. Nevertheless, this problem has been partially resolved by including participants ID as a random factor during the statistical modelling of the data, which should have reduced the impact of this limitation.

To summarise, three limitations of the paradigm used in this thesis have been identified: 1) lack of information as to whether effort–based decision-making in the lab can be predictive/diagnostic of general patterns of effort expenditure in mental/physical task, 2) uncertainty as to whether methods of measurement used reflect actual effort exertion, and 3) lack of adjustment in the effort requirements of the task. Nevertheless, regardless of these limitations, the results of the studies presented in this thesis provide a strong support for utilising V-E-D-M framework during investigations of effort-based decision-making.

7.8 Summary

Effort-based decision-making is a process of deciding between options associated with different levels of rewards and effort. Considering the importance of this process for our everyday functioning, it has been relatively underinvestigated so far. Therefore, the main aim of this thesis was to explore the factors that determine behaviour during effort-based decision-making. To that end, a novel framework for investigating this process, the V-E-D-M model, was proposed. The model assumed that effort-based decision-making consists of six separate stages: Representation, Valuation, Action Selection, Action Execution, Outcome Evaluation, and Learning. Behaviour during these stages was thought to depend on the characteristics of the decision-making problem, particularly reward magnitude, valence, and reliability, effort type, feedback type, and timing of Action Execution, as well as the levels of dopamine in the brain of decision-maker. However, the exact effects of these factors on the effort-based decision-making process were unclear. For that reason, six experiments investigating the influence of reward, effort, and feedback on performance during effort-based decision-making were designed and implemented.

These experiments were conducted using a novel effort-based decision-making task consisting of three phases: Training phase, Choice phase, and Execution phase. During Training and Execution participants were required to put in physical effort (squeeze the hand grip device) or mental effort (solve simple mathematical equations) to obtain small monetary rewards. During Choice, participants had a chance to choose between options associated with different levels of effort and reward. Participants' choices, effort exertion, and accuracy during the task were analysed to establish the impact of effort, reward, and feedback, as well as dopamine depletion on effort-based decision-making, with the aim of assessing the validity of the assumptions of the V-E-D-M model.

The results of these investigations showed that: 1) the effects of reward magnitude on effort-based decision-making depend on the stage of the process, as rewards seem to affect behaviour mainly during Action Selection, and less so during Action Execution; furthermore, relative reward values seem to matter more than absolute reward values, 2) changing reward valence affects effort-based decision-making, as people become more risk averse when losses are at stake, 3) reward reliability can potentially affect effort-based decision-making, but only when participants believe they can increase their chances of obtaining rewards through exerting effort, 4) reward values drive behaviour during Action Selection, whereas effort requirements determine behaviour during Action Execution, 5) increasing the informative value of outcome feedback does not affect effort-based decision making, 6) delaying Action Execution affects effort exertion during this stage. These findings have been incorporated into the revised V-E-D-M model.

In conclusion, the investigations presented in this thesis clarify the effects of manipulating reward, effort and feedback on effort-based decision-making. They also point to the usefulness of the V-E-D-M model for investigating this process. At the same time, they suggest areas that still need to be investigated in order to increase the predictive power of this model, providing interesting avenues for future research.

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APPENDIX A

Description of the exact data analysis methods used in the six experiments forming an empirical part of this thesis.

<u>Choice</u>

Experiment 1 (Gains)

Physical Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, and Feedback were included into the full model. Additionally, interactions between Effort Level*Reward Level, Reward Feedback*Effort Level, Reward Feedback*Reward Level, and Reward Feedback*Effort Level*Reward Level were included. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, and Effort Level*Reward Level interaction as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, and Reward Feedback were included in the full model. Additionally, interactions between Effort Level*Reward Level, Reward Feedback*Effort Level, Reward Feedback*Reward Level, Reward Feedback*Effort Level*Reward Level were included. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, and Effort Level*Reward Level interaction as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Effort Type and Reward Feedback, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, Effort Type, as well as Effort Level*Reward Level and Effort Type*Effort Level interactions as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 2 (Losses)

Physical Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Attractiveness, and Reward Valence, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Attractiveness and Reward Valence, as well as Effort Level*Attractiveness, Reward Valence*Effort Level and Reward Valence*Attractiveness interactions as fixed effects. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Attractiveness, and Reward Valence, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Attractiveness and Reward Valence, as well as Effort Level*Attractiveness, Reward Valence*Effort Level and Reward Valence*Attractiveness interactions as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Reward Valence and Effort Type as well as all the possible interactions between them, were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all factors except for Effort

Type*Reward Valence*Attractiveness and Effort Type*Reward Valence*Effort Level*Attractiveness interactions as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 3 (Reliability)

Physical Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, and Reward Reliability, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, Reward Reliability, as well as Effort Level*Reward Level, and Reward Reliability*Effort Level interactions as fixed effects. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, and Reward Reliability, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, Reward Reliability, as well as Effort Level*Reward Level, and Reward Reliability*Effort Level interactions as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Reward Reliability and Effort Type, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all factors except for Effort Type*Reward Reliability*Reward Level and Effort Type*Reward Reliability*Effort Level*Reward Level interactions. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 4 (Increased Incentives)

Physical Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Reward Reliability and Reward Magnitude, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, Reward Reliability, as well as interactions between Effort Level*Reward Level, Reward Reliability*Effort Level, and Reward Reliability*Reward Level as fixed effects. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Reward Reliability and Reward Magnitude, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, Reward Reliability, as well as Effort Level*Reward Level, Reward Reliability*Effort Level, and Reward Reliability*Reward Level interactions as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Reward Magnitude and Effort Type, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, and Effort Type, as well as and Effort Level*Reward Level and Effort Type*Effort Level interactions as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 5 (Immediate Execution)

Physical Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Reward Feedback and Timing of Execution, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level and Effort Level*Reward Level interaction as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Reward Feedback and Timing of Execution, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level and Effort Level*Reward Level interaction as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Timing of Execution and Effort Type, as well as all the possible interactions between them were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, and Effort Type, as well as and Effort Level*Reward Level and Effort Type*Effort Level interactions as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 6 (PD study)

Physical Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, and Group, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, and Group, as well as interactions between Effort Level*Reward Level and Group*Effort Level as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, and Group, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level and Reward Level, as well as Effort Level*Reward Level interaction as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary (option chosen vs. option rejected), GLMM assuming binomial distribution was used to analyse the choice data. Fixed effects of Effort Level, Reward Level, Group and Effort Type, as well as all the possible interactions between themwere included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level and Reward Level, as well as Effort Level*Reward Level interaction as fixed factors. As the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom indicated overdispertion, a random factor for each observation was included in the model. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Effort Exertion

Experiment 1 (Gains)

Physical Effort

LMM approach was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, and Reward Feedback, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Visual inspection of residual plots suggested potential violation of normality assumption. Consequently, strength data was transformed using square root transformation of reversed scores. Residuals of subsequent models showed no indication of violating the assumption of homoscedasticity or normality. The final model, selected based on the AIC criterion, included Effort Level as the only fixed effect. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

LMM approach was initially used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, and Reward Feedback, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. However, visual inspection of residual plots of the full model indicated violation of assumption of homoscedasticity and normality, and the data could not be transformed to normality. For that reason GLMM assuming gamma distribution with inverse link function was employed instead of LMM. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level as the only fixed factor. Model diagnostics gave no indication of non-constant variance or overdispertion.

Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test the fixed effect.

Experiment 2 (Losses)

Physical Effort

LMM approach was used to deal with repeated measures. Fixed factors of Effort Level, Stakes Level, and Reward Valence, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Visual inspection of residual plots suggested potential violation of homoscedasticity assumption. Consequently, strength data was transformed using square root transformation of reversed scores. Residuals of subsequent models showed no indication of violating the assumption of homoscedasticity. Based on the AIC criterion the final model was selected which included Effort Level, Stakes Level and Effort Level*Stakes Level interaction as fixed factors. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

Since RT data had a significant positive skew, and could not be normalized using standard transformations, GLMM approach assuming gamma distribution with logarithmic link function was used to deal with repeated measures. Fixed effects of Effort Level, Stakes Level, and Reward Valence, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors except for Reward Valence*Effort Level*Stakes Level interaction. Model diagnostics gave no indication of overdispertion or non-constant variance. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test the fixed effect.

Experiment 3 (Reliability)

Physical Effort

LMM approach was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, and Reward Reliability, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Visual inspection of residual plots suggested that homoscedasticity assumption was violated. Consequently, strength data was transformed using square root transformation of reverse scores. Residuals of subsequent models showed no indication of violating the assumption of homoscedasticity or normality. Based on the AIC criterion the final model was selected which included Effort Level as the only fixed factor. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was not normally distributed, GLMM assuming gamma distribution family with inverse link was implemented to analyse the RT data. Fixed effects of Effort Level, Reward Level, and Reward Reliability, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level as the only fixed factor. Model diagnostics did not reveal any indication of overdispertion or non-constant variance. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 4 (Increased Incentives)

Physical Effort

LMM approach was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, Reward Reliability and Reward Magnitude, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Visual inspection of residual plots suggested a potential violation of homoscedasticity assumption. Consequently, the strength data was transformed using the square root transformation of reversed scores. Residuals of subsequent models showed no indication of violating the assumption of homoscedasticity. Based on the AIC criterion the final model was selected which included Effort Level and Reward Level as fixed factors. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

Since RT data had a significant positive skew, and could not be normalized using standard transformations, GLMM approach assuming gamma distribution with logarithmic link function was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, Reward Reliability and Reward Magnitude, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level and Reward Magnitude, as well as Effort Level*Reward Level, Reward Magnitude*Effort Level and Reward Magnitude*Reward Level interactions as fixed factors. Model diagnostics gave no indication of overdispertion or non-constant variance. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test the fixed effect.

Experiment 5 (Immediate Execution)

Physical Effort

LMM approach was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, Reward Feedback and Timing of Execution were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Visual inspection of residual plots suggested a potential violation of homoscedasticity assumption. Consequently, the strength data was transformed using the square root transformation of reversed scores. Residuals of subsequent models showed indication of violating the assumption of homoscedasticity. Based on the AIC criterion the final model was selected which included Effort Level, Reward Level, and Timing of Execution as well as Effort Level*Reward Level and Timing of Execution*Effort Level interactions as fixed factors. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

Since RT data had a significant positive skew, and could not be normalized using standard transformations, GLMM approach assuming Gamma distribution with logarithmic link was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, Reward Feedback and Timing of Execution, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level and Timing of Execution, as well as Effort Level*Reward Level and Timing of Execution*Effort Level interactions as fixed factors. Model diagnostics gave no indication of overdispertion or non-constant variance. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test the fixed effect.

Experiment 6 (PD study)

Physical Effort

LMM approach was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, and Group, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. As the visual inspection of residual plots indicated the violation of homoscedasticity assumption, the strength data was transformed using square root transformation of reversed scores. Visual inspection of residual plots of the subsequent models did not reveal any obvious deviations from homoscedasticity or normality. Based on the AIC criterion the final model was selected which included Effort Level as the only fixed factor. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

LMM approach was used to deal with repeated measures. Fixed factors of Effort Level, Reward Level, and Group, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. As the visual inspection of residual plots of the resulting model indicated violation of homoscedasticity assumption, RT data was transformed using logarithmic transformation. Visual inspection of residual plots of the subsequent models did not reveal any obvious deviations from homoscedasticity or normality. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion model which included Effort Level and Reward Level, as well as Effort Level*Reward Level interaction as fixed factors was chosen. Maximum Likelihood method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Accuracy

Experiment 1 (Gains)

Physical Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, and Reward Feedback, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level and Reward Level as fixed factors. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was implemented to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, and Reward Feedback, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level as the only fixed effect. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Effort Type and Reward Feedback, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors except for Effort Type*Reward Feedback*Effort Level*Reward Level interaction. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 2 (Losses)

Physical Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Stakes Level and Reward Valence, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors except for Reward Valence*Effort Level*Stakes Level interaction. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Stakes Level and Reward Valence were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors except for Reward Valence*Effort Level*Stakes Level interaction. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Stakes Level, Effort Type and Reward Feedback, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 3 (Reliability)

Physical Effort

As all participants were found to be 100% accurate on low effort trials, the estimation of predictor coefficients was not possible (The model would not converge). Consequently, low effort trials were excluded from the analysis. As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Reward Level and Reward Reliability, as well as an interaction between them were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Reward Level as the only fixed factor. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was implemented to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, and Reward Reliability, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level as the only fixed factor. There was some indication of overdispertion in the model, based on the analysis of the ratio between the sum of squared Pearson residuals and the residual degrees of freedom, so a random factor of Observation was included in the model as well. There was no indication of overdispertion in the resulting model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Effort Type and Reward Reliability, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors except for Effort Type*Reward Level, Effort Type*Reward Reliability*Effort Level, Effort Type*Reward Reliability*Reward Level, and Effort Type*Reward Reliability*Effort Level*Reward Level interactions. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 4 (Increased Incentives)

Physical Effort

As all but one participant were found to be 100% accurate on low effort trials, the estimation of predictor coefficients was not possible (the model would not converge). Consequently, low effort trials were excluded from the analysis. As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Reward Level, Reward Reliability and Reward Magnitude were included into the full model. Participant ID was included into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Reward Level and Reward Magnitude as fixed factors. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was implemented to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Reward Reliability and Reward Magnitude, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, Reward Reliability and Reward Magnitude as well as interactions between Effort Level*Reward Level, Reward Magnitude*Effort Level, Reward Magnitude*Reward Level, and Reward Magnitude*Effort Level*Reward Level as fixed factors. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Effort Type and Reward Magnitude, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors except for Effort Type*Reward Reliability*Reward Level and Effort Type*Reward Reliability*Effort Level*Reward Level interactions. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 5 (Immediate Execution)

Physical Effort

As the outcome variable was binary, GLMM assuming binomial distribution was implemented to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Reward Feedback and Timing of Execution, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level and Reward Level as fixed effects. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was implemented to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Reward Feedback and Timing of Execution, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level, Timing of Execution as well as interactions between Effort Level*Reward Level and Timing of Execution*Effort Level as the fixed factors. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Effort Type and Timing of Execution, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors. There was no indication of overdispertion in the model.

Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Experiment 6 (PD study)

Physical Effort

As the outcome variable was binary, GLMM assuming binomial distribution was implemented to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, and Group, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level, Reward Level and Effort Level*Reward Level interaction as fixed effects. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was implemented to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, and Group, as well as all possible interactions were included into the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included Effort Level as the only fixed effect. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

Physical vs. Mental Effort

As the outcome variable was binary, GLMM assuming binomial distribution was used to analyse the accuracy data. Fixed factors of Effort Level, Reward Level, Effort Type and Group, as well as all possible interactions were included in the full model. Participant ID was incorporated into the model as a random factor, to account for repeated measures. Backward method of variable selection was used to create models of different complexity, and information theoretic tool (AIC) was used to select the model with the highest estimated predictive power. Based on this criterion the final model was selected which included all fixed factors except for the interactions between Effort Type*Group*Effort Level, Effort Type*Group*Reward Level, and Effort Type*Group*Effort Level*Reward Level. There was no indication of overdispertion in the model. Maximum Likelihood (Laplace Approximation) method was used to estimate the parameters of the model. Likelihood ratio test was used to test fixed effects.

APPENDIX B

Tables presenting descriptive statistics regarding choice, effort exertion and execution.

Table B1. Percentage of times each option (i.e. HEHR, HELR, LEHR, LELR) was chosen on trials during which it was available during the Choice phase.

Experiment	Mental Effort				Physical Effort			
	HEHR Mean (SD)	HELR Mean (SD)	LEHR Mean (SD)	LELR Mean (SD)	HEHR Mean (SD)	HELR Mean (SD)	LEHR Mean (SD)	LELR Mean (SD)
Experiment 1 (Gains)	62.43% (13.76)	4.58% (8.10)	92.95% (10.80)	39.86% (14.38)	71.87% (14.49)	5.87% (9.57)	88.05% (13.32)	34.27% (11.24)
Experiment 2 (Losses)	53.52% (17.41)	3.71% (7.37)	94.78% (10.25)	47.01% (16.80)	60.38% (22.89)	4.65% (8.92)	91.64% (12.42)	44.14% (17.93)
Experiment 3 (Reliability)	69.14% (17.80)	10.04% (16.60)	86.82% (18.65)	32.55% (15.85)	67.54% (16.85)	12.93% (19.17)	86.42% (17.30)	34.29% (18.34)
Experiment 4 (Increased Incentives)	66.00% (17.68)	9.06% (15.57)	87.73% (17.32)	35.96% (18.07)	69.29% (17.29)	12.99% (18.71)	85.28% (18.39)	32.69% (17.15)
Experiment 5 (Immediate Execution)	63.21% (13.04)	4.61% (1.79)	93.69% (9.41)	38.22% (13.85)	73.48% (15.45)	6.12% (1.56)	88.98% (11.95)	31.69% (12.37)
Experiment 6 (PD study)	50.41% (13.75)	13.98% (11.34)	68.17% (16.99)	39.63% (14.83)	55.49% (13.67)	16.08% (12.18)	65.42% (18.26)	38.67% (12.46)

Table B2. Average response times and grip strength values on different types of trials (i.e. HEHR, HELR, LEHR, LELR) during the Execution Phase.

Experiment	**Mental Effort**				**Physical Effort**			
	HEHR Mean (SD)	**HELR Mean (SD)**	**LEHR Mean (SD)**	**LELR Mean (SD)**	**HEHR Mean (SD)**	**HELR Mean (SD)**	**LEHR Mean (SD)**	**LELR Mean (SD)**
Experiment 1 (Gains)	2.27s (0.79)	2.45s (0.83)	0.99s (0.14)	0.95s (0.26)	85.75N (4.94)	76.68N (15.48)	58.51N (19.86)	58.61N (20.31)
Experiment 2 (Losses)	3.05s (1.04)	3.01s (1.01)	1.30s (0.52)	1.47s (0.61)	85.18N (5.37)	79.21N (9.90)	59.56N (16.02)	59.71N (16.28)
Experiment 3 (Reliability)	3.00s (0.77)	3.15s (0.85)	0.98s (0.17)	0.97s (0.21)	82.31N (4.57)	80.18N (7.13)	58.62N (11.50)	57.60N (13.20)
Experiment 4 (Increased Incentives)	3.10s (0.73)	3.07s (0.78)	1.32s (0.52)	1.27s (0.47)	82.38N (3.81)	80.64N (6.11)	58.23N (11.99)	56.81N (13.64)
Experiment 5 (Immediate Execution)	2.58s (0.78)	2.89s (090)	1.33s (0.51)	1.33s (0.56)	83.35N (5.44)	76.58N (12.97)	58.09N (17.35)	56.56N (17.83)
Experiment 6 (PD study)	4.25s (0.50)	4.13s (0.56)	2.24s (0.40)	2.06s (0.32)	79.53N (7.43)	79.00N (7.43)	53.71N (18.60)	51.78N (18.80)

Table B3. Accuracy on different types of trials (i.e. HEHR, HELR, LEHR, LELR) during the Execution Phase.

Experiment	Mental Effort				Physical Effort			
	HEHR Mean (SD)	HELR Mean (SD)	LEHR Mean (SD)	LELR Mean (SD)	HEHR Mean (SD)	HELR Mean (SD)	LEHR Mean (SD)	LELR Mean (SD)
Experiment 1 (Gains)	57.87% (25.94)	49.40% (44.87)	72.87% (14.62)	72.56% (21.68)	85.12% (20.57)	59.55% (43.51)	100%	99.39% (3.90)
Experiment 2 (Losses)	58.84% (30.59)	57.72% (31.78)	82.13% (15.87)	79.85% (20.25)	84.50% (23.09)	73.62% (32.51)	99.62% (1.01)	98.89% (4.57)
Experiment 3 (Reliability)	51.21% (31.48)	42.41% (41.47)	72.50% (15.49)	79.61% (23.51)	83.86% (19.90)	65.66% (41.14)	100%	100%
Experiment 4 (Increased Incentives)	52.28% (32.11)	47.50% (42.67)	80% (16.64)	84.82% (21.04)	87.61% (17.16)	74.93% (36.23)	99.88% (0.99)	100%
Experiment 5 (Immediate Execution)	57.22% (28.92)	44.47% (46.24)	80.59% (15.02)	80.97% (21.83)	87.35% (19.65)	67.59% (42.96)	1	99.66% (2.93)
Experiment 6 (PD study)	57.88% (25.44)	62.19% (33.15)	94.41% (6.77)	98.39% (4.95)	97.64% (6.41)	88.45% (16.89)	98.79% (3.80)	98.39% (4.95)