Decision-making during action

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Abstract

Decision making requires coordinating motor actions that are necessary to report the choices and sample relevant information from the environment. For instance, when riding a bike on a busy road, rider must both pedal while deliberating over the upcoming sensory information in order to make subsequent decisions about when to make a turn. Embodied decision making is a recent framework that aims to investigate such situations and understand the links between our actions and decisions. This doctoral thesis takes embodied decision accounts as a central theoretical stance and studies various important aspects of decision making during motor action. The main locus of this research is to understand how actions that are needed for evidence accumulation influence and interact with the decision making process. To this end, we present here three experimental works and their results. In the first study, we found that sampling movements and response related movements are subject to online interaction during a categorical decision making task. In the second study, we delved into how physical effort of actions that are required to sustain stimuli influence the speed and accuracy of responses. The results showed that effort induced faster and less accurate decisions similar to strict time constraints. We concluded that effort induces urgency over decision making. In the final study, our goal was to test whether physical effort induce higher arousal levels which might have a role in updating speed and accuracy trade-off under effortful actions. The data showed that tonic pupil sizes (an index for arousal) was significantly modulated by effort and correlated with speed and accuracy of responses. Overall, these findings contributed novel evidences on the links between action and decision, especially in cases when evidence accumulation is bound to motor actions.

Resum

La presa de decisions requereix coordinar les accions motrius necessàries per indicar implementar les decisions preses, i les que ajuden a adquirir informació de l'entorn. Per exemple, quan es va en bicicleta per un carrer transitat, el ciclista ha de pedalar alhora que delibera sobre la informació sensorial que rep per poder anar prenent decisions sobre els girs i frenades. La presa de decisions incorporada (*embodied decision making)* és un àmbit d'estudi recent que pretén investigar aquestes situacions i entendre els vincles entre les accions i les decisions del subjecte en el seu entorn. Aquesta tesi doctoral pren les teories de la presa de decisions incorporada (*embodied decision accounts)* com a posició teòrica primària, per adreçar diversos aspectes de la presa de decisions durant l'acció motriu. El focus principal d'aquesta investigació és entendre com les accions necessàries per a l'acumulació d'evidència influeixen i interactuen amb el procés de presa de decisions. Amb aquesta finalitat, es presenten tres treballs experimentals i els seus resultats. En el primer estudi, vàrem trobar que els moviments de mostreig d'informació i els moviments relacionats amb la resposta interactuen sobre la marxa durant la tasca de presa de decisions categòrica. En el segon estudi, vàrem aprofundir en com l'esforç físic d' accions que son necessàries per mantenir la visibilitat de la informació rellevant influeixen en la velocitat i la precisió de les respostes. Els resultats varen mostrar que l'esforç indueix decisions més ràpides i menys precises, de forma similar al que passa quan s'imposen limitacions de temps. Vàrem concloure que l'esforç indueix urgència en la presa de decisions. En l'estudi final, el nostre objectiu era provar si l'esforç físic indueix un increment dels nivells d'excitació (*arousal*), que podrien tenir un paper en la velocitat i la variació de la precisió durant les decisions amb esforç. Les dades varen reflectir que la resposta pupil·lar tònica (un índex d'excitació) estaven modulades significativament per l'esforç i correlacionades amb la velocitat i la precisió de les respostes. En general, aquests resultats aporten evidències innovadores sobre els vincles entre l'acció i la decisió, especialment en els casos en què l'acumulació d'evidència sensorial està lligada a accions motrius.

Table of contents

1. INTRODUCTION

In real life, humans and other animals face countless situations in which they have to decide at the same time as there are acting upon their environments. From survival situations such as running away from a predator, to complex human behavior like driving and riding a bike, organisms must coordinate their movements while making the cognitive operations regarding choices to carry out the task at hand. In cognitive neuroscience and psychology, the notions of sensorimotor coupling and embodied interactions have started to gain interest in the last few decades. Before these trends in the field, the dominant theories about cognition focused mostly on abstract operations in isolation from the body and motor aspects (Piaget, 1960, Skinner, 1965). Although these classic accounts have generated many insights about cognition, these approaches have been critiqued because, in ecological situations, the abstract cognitive processes coexist and interact with physical movement, planning, and execution of actions (Shapiro, 2011). Thus, it was inevitable to build a new research agenda which focuses on those interactions.

Increased interest in bodily processes in relation to cognitive abilities became a scientific framework which can be summarized as Embodied Cognition (Clark, 1999). Embodied Cognition accounts have incorporated existing knowledge that had been somehow remained silent under the conventional accounts in psychology and cognitive science. For instance, decades before

Embodied Cognition have been utilized as a term, Carpenter (1874) had a ‘ideo-motor theory’ whose main premise was considering ideas and actions as a coupled and iterative processes. However, his approach had been criticized heavily and did not reach a mainstream acceptance under the behaviorist and Gestalt views of psychology which looked at cognition from manifest, observable behaviors or operations detached from the bodily realm (Prinz, 1974). Another influential account was Gibson’s Ecological Psychology which brought about the concept of affordances; direct perception of actionable characteristics in objects and phenomena (Gibson, 1961, Gibson, 1977). Gibson’s view highlighted that cognition and perception are dynamics that can be traced back to motor actions which are realized, planned or merely perceived. Gibson’s view influenced linguists which brought the idea that linguistic concepts are grounded in the action-perception loops (Lakoff & Johnson, 1980), and also roboticists who positioned bodily interactions as a central piece in mental operations (Van Gelder, 1995, Thelen & Smith, 1996). Later in 2000s, Profitt (2006) coined the term Embodied Perception which emphasized the perception’s role in serving movements and Barsalou (2008) discussed ‘Grounded Cognition’ by postulating that bodily states and external states controlling what we call cognition. In the last years, embodied stances have been complemented with research that focuses on the links between physiological processes and cognition. For example, Azallini and colleauges (2021) found that cortical rhythm was modulated by heart beats and this influenced the decisions human make. Furthermore, there is also evidence which suggest that gastric contractions influence the brain rhythms and therefore have implications for cognition (Rebollo et al., 2021). From this brief summary, it is evident that there have been numerous attempts to bridge the gap between bodily processes and cognitive processes.

There are different manifestations of embodied views of cognition depending on specific questions and subfields at hand. Although embodied mind has gained popularity in linguistics, robotics and artificial intelligence (Clark, 1999), the study of decision making remained to be dominated by classic accounts for a very long time. The classic view of decision making posits that decision follows separate stages in a sequential order; namely deliberation, deciding and executing response (Ratcliff & McKoon, 2008). This serial understanding had influenced the majority of decision making models which were fruitful to explain mechanistic sub-dynamics such as evidence accumulation and response execution. However, scholars have realized that many ecological situations necessitate, or at least allow, acting and deciding at the same time (Cisek & Pastor-Bernier, 2014). Therefore, we have observed a similar trend in the decision making field as in cognitive science in general, about increased attempts to incorporate bodily action dynamics into the understanding of decisions (Gallivan et. al., 2018, Lepora & Pezzulo, 2015, Cisek, 2019). According to these embodied accounts of decision making, action and decisions interact continuously. This claim was also empirically supported by experimental setups which allowed to track continuous movement dynamics (Burk et. al., 2014, Carsten et. al., 2022). By using robotic handles (Figure 1A) or computer mouse (Figure 1C), these studies try to infer decision processes from the shape of movements (Stone et. al., 2022, Schoemann et. al., 2019). Hence, the experimental paradigms which involved continuous movements in a decision making setting have been crucial to bolster the central claim that decision and action can take place at the same time.

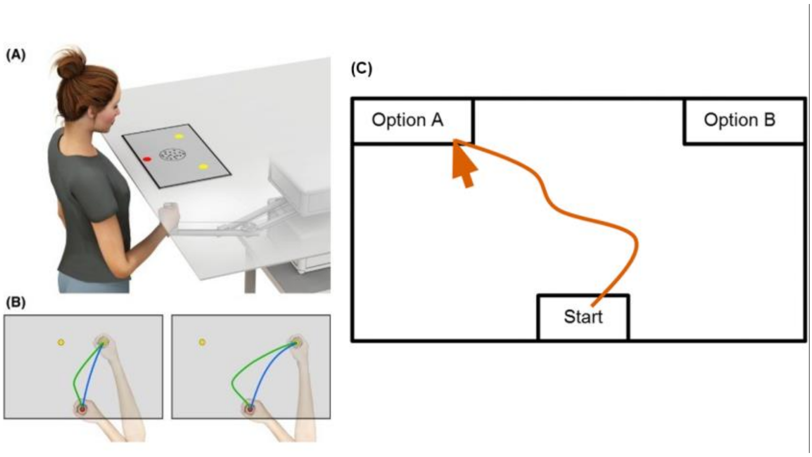

Figure 1. Examples for continuous movement paradigms. (A) and (B) are from Stone et. al., (2022) and (C) is from Schoemann et. al., (2019).

In this thesis, my goal was to delve into action-decision interactions and provide new understanding about some uncharted aspects of the embodied decision making framework. In Chapter 2.1. we present our experimental work which involved a novel continuous movement paradigm with an active sampling component. After settling down how sampling actions and response actions interact simultaneously, we moved on to studying whether effort of the actions can be a critical factor in decision making (Chapter 2.2.).

Finally, we took it one step further and investigated if effort of actions modulate arousal which in turn end up in modulating speed and accuracy of responses (Chapter 2.3.). In each of the sections of Chapter 2, we provide detailed literature review of the current knowledge about the related questions. In the following sections of this chapter we demonstrate the conceptual context of this thesis work and our hypothesis. Finally, in the last chapter (Chapter 3), we discuss the overall conclusions from this thesis and corroborate relevant contributions of our work into the field.

1.1 Cost of actions in relation to decision-making

Decision making has been highly influenced by optimality constraints. As the goal in a decision is to pick the best option among all the available alternatives, one needs to consider both the rewards and the costs of each option (Rigoux & Guigon, 2012). For the scope of this thesis, we focus on the costs of actions as an important factor in optimal decisions. According to economic decision making theories, the cost of a response action has to be incorporated into the deliberation process in order to avoid expending too much energy for a reward (Shadmehr, 2010). The experimental work under this approach has shown that when a decision maker has to choose between two actions with equal rewards, they choose the one with the least motor cost (Rosenbaum, 2012, Cos, Medleg, Cisek, 2012). To allow for the consideration of action costs prior to choice, the brain has to come up with predictions about these costs during the deliberation stage. When a single, ballistic movement is needed to respond, the estimation of predicted costs is relatively simple, compared to cases in which a dynamic, continuous movement is required. In fact, most of the ecological situations involve continuous actions which require an online cost tracking mechanism. Optimal Feedback Control (OFC) framework under motor control field focuses on the mechanisms of calculating and carrying out movement plans in an optimal way. Although OFC was initially thought to be a theory solely about motor control, many scholars have used the principles of OFC in decision making context (Krakauer, 2019) and this has helped to cast optimality principles an important role in choices (Trommershauser, J., Maloney, L. T., & Landy, M. S. 2003).

Approaches which bridged the OFC theory and decision making involved experimental paradigms with continuous movement tracking (Todorov, 2004, McKinstry et. al., 2008, Chapman et. al., 2010, Klaes et. al., 2011). Reporting response via moving a joystick or a robotic handle to a certain distal point, these type of paradigms allowed analyzing the movement trajectories. This thus enabled studying the simultaneous dynamics in online movement planning and decision making (Song & Nakayama, 2008, Wood et. al., 2013). One central take away message from these approaches is that the decision process continues during the movement execution and, importantly, movement plans can also be updated during this deliberation stage (Michalski et. al., 2020). This was in accordance with the intuitions derived from OFC that action processing is not a mindless operation, but rather it exhibits all sorts of cost calculations and updating mechanisms and strong communication with cognitive processes (Rigoux & Guigon, 2012).

1.2 Cost of sampling actions in relation to decision-making

Up until here, I have discussed the cost of actions which are necessary to report choices. On top of executing responses, actions are also needed to sample information from the environment, which in turn inform the decisions. In neuroscience, eye-movements have been studied with their role in sampling visual information under the sub-field of active vision (Yarbus, 1967, Goodale, 1983, Barnes, 2008, Friston et. al., 2010). Thanks to research in active vision, we now know that action and perception operate with interactive feedforward and feedback loops (Goodale, 2011). Although eye movements are the fundamental information gathering actions in humans and primates, at least in vision, they are quite ‘cheap’ actions which do not expend too much energy. However, other actions which involve multiple and bigger muscle groups are also significant in extracting information from the environment. For instance, to find food sources in an environment, an animal must move its body around (through obstacles, up-hill, down-hill, etc.) or avoiding a predator requires moving and looking for routes or shelters. We can claim that navigation in general involves energy-expensive movements which are aimed towards exploring and exploiting the environment. Reinforcement Learning has used methods and paradigms that posits the exploration-exploitation mechanism as its central component (Sutton & Barto, 1998, Kearns

& Singh, 2002). Despite the machine learning aims to implement systems with the notions of sampling cost of information, there is still a lot to understand about the behavioral dynamics of the cost of sampling actions (in terms of metabolic costs) and its interaction with decision processes. Especially, novel decision-making paradigms with active sampling components would be fruitful for the understanding of action-decision relationship.

1.3 Effort as a currency in decision-making

In the last two sections above, we briefly summarized the role of action costs in decision making, yet we did not specify the types of costs pertaining to actions. Action planning, action monitoring and action updating are all costly processes which are examples of action-related costs. However, one central component of action costs is the effort of the movement. Effort involves the metabolic cost of implementing an action which can trivially impact the economics of a decision making (Walton et. al., 2007, Croxson et. al., 2009, Hillman & Bilkey, 2010). De Froment et. al., (2014) have postulated that physical effort should be added into the common research agenda of decision-making which traditionally focus mostly on speed and accuracy trade-offs. Thus, they recommended adding effort as the third variable into the speed-accuracy trade-off and study the three-way trade-off between speed, accuracy and effort. Although theirs is only a theoretical claim, there are also empirical studies which tested and investigated the effort’s influence on decisions. For instance, Prevost et. al. (2010) have shown that humans in a delayed reward task showed a preference to choose larger effort to wait shorter, which shows an example to trading off effort with time. Other researchers as well supported with their experimental work that decision making and motor control share a common principle of maximizing utility (Shadmehr et. al., 2016, Morel et. al., 2017). Similar to delay discounting (reduced reward value under long delays, i.e. Rachlin, 2006), effort-discounting is an important mechanism which reduces the value of rewards as a function of the physical effort of obtaining those rewards (Sugiwaka & Okouchi, 2004, Hartmann et. al., 2013, Nishiyama, 2016).

As empirical works have established the effort discounting as a utility factor in decision making, a critical question emerged about the potential neural underpinnings of this phenomena. Klein-Flugge et. al., (2016) have conducted an fMRI study in which human participants needed to make choices between options which had varying amounts of effort and rewards. They found that supplementary motor area and dorsal anterior cingulate cortex (ACC) were involved in calculating and comparing of the reward/cost of the options. Similar other studies also reported the activity of ACC as enabling the utility maximizations and effort discounting (Arulpragasam et. al., 2018, Chong et. al., 2017, Bernacer et. al., 2019). Under the light of these evidences, we can conclude that effort is a currency that needs to be processed for the service of achieving optimal decisions and this takes place within the brain networks which play a role in cost/value calculation.

1.4 Arousal modulations due to effortful actions

It is plausible to expect that effortful motor actions would induce global changes into the brain due to heightened parasympathetic activity and hemodynamic changes in the body. Amongst them, arousal can be defined as a complex system that relates to a global brain state linked to wakefulness, attention and performance in various tasks (Aston-Jones & Cohen, 2005). It is believed that arousal is driven by norepinephrine (NE) and cholinergic (Ach) releases from Locus Coeruleus (LC) and basal forebrain, respectively (Berridge & Waterhouse, 2003). It is also known that pupil of the eye shows strong modulations correlated with the activations in LC and therefore correlated with arousal. Therefore, pupil-linked arousal is studied intensively in domains of neuroscience and psychology due to noninvasive measurement technique of pupillometry.

Although arousal is known to be modulated by sleep cycles, emotions and mental effort (Berridge & Waterhouse, 2003, Howells et. al., 2012), there was not a direct test of how physical effort induces arousal changes until recently. Schmidt et. al., (2012) compared cognitive and physical effort in terms of their MRI activity patterns and reported that Ventral Striatum (VS) activity was showing significant modulation as a function of effort. Specifically, they reported a higher activity in caudate nucleus in high mental efforts and higher activity in putamen in high physical effort conditions. Since VS receives input from LC which has an important role in NE release and arousal, their result hinted the potential arousal modulations under both cognitive and physical effort. However, even the study of Schmidt et. al. (2012) was not directly testing arousal. The first study we could find that looked at physical effort and arousal relationship is the work of Zenon et. al., (2014). The researchers have conducted an effort-production experiment in which they measured pupil size. They found that similar to cognitive effort, physical effort was inducing systematic changes to pupil size, namely increasing the arousal as a function of effort intensity. Similarly, Varazzani et. al., (2015) have conducted a neural recording study in which monkeys squeezed a bar with their hands in different force levels. They reported an increased LC activity with higher effort levels and this relationship was also correlated with the pupil sizes. Therefore, they concluded that noradrenergic arousal system has a unique relationship with physical effort, and extrapolated that this mechanism allows organisms to face physical challenges and energize their behavior. Taking the evidences for arousal and effort relationship, and remembering that arousal impacts the overall brain, it is a plausible claim that arousal due to physical effort can have indications for decision making.

1.5 Scope and hypotheses

The overarching hypothesis of this dissertation is that actions that are coupled with evidence accumulation influence and interact with the decision making process. Under this broad hypothesis, specific paradigms to answer more detailed questions were generated. In the following sections, I will demonstrate the hypotheses of each study under this thesis work and explain the main goals.

1.5.1. Active sampling and decision-making can happen simultaneously

According to embodied views of decision making, rich connections between actions and decisions allow organisms to successfully incorporate movements that bring about sensory information necessary to reach a decision (e.g., Lepora & Pezzulo, 2015). However, there was not a direct empirical test of this theoretical preposition. In the first study under this thesis, we aimed to fill this gap by implementing a decision making experiment in which movements could bring new sensory information. We developed a novel experimental paradigm that involved moving a computer mouse in order to reveal information about the visual stimulus and also to report choice. The hypothesis of our work in Chapter 2.1. was that actions related to decision making and actions related to sampling of information are subject to online interaction. In the context of our work, we predicted to observe markers of sampling movements and response movements happening in the same time window.

1.5.2. Physical effort influences speed and accuracy in decision-making

In the second study (Chapter 2.2.), we moved into another important facet of action-decision interaction. As described in the previous sections, physical effort of actions influences the optimality dynamics in decision making process. There is already a well-known mechanism in decision making that is proposed to implement time-related optimizations, which is ‘urgency’ (Thura et. al., 2012). In Chapter 2.2., we draw possible connections between urgency that time constraints induce and urgency that a costly action may introduce. Our hypothesis was that physical effort imposes urgency similar to time-constraints. In order to draw comparisons between time-based and effort-based urgency, we manipulated both the response deadline and the amount of physical effort in a perceptual discrimination task. Our prediction was that we would find changes in speed and accuracy of responses under increased effort, similar to that of under short deadlines.

1.5.3. Arousal due to physical effort correlates with speed and accuracy trade-off

In the final study (Chapter 2.3.), we built over the results we obtained from the second study (Chapter 2.2.) and tried to disentangle the dynamics behind speed and accuracy changes under physical effort. As arousal is inevitable when an organism is involved in a strenuous action, we corroborated that physical effort’s influence on SAT might be mediated by arousal modulations. We used the same experimental paradigm as in Chapter 2.2. with the addition of pupil recording during the sessions. The main hypothesis was that physical effort alters pupil-linked arousal as well as modulating speed and accuracy trade-off. Thus, we predicted to see differences in tonic pupil sizes as a function of effort levels and to show a correlation between the pupil size modulations and SAT modulations due to effort.

2. EXPERIMENTAL STUDIES

2.1. The dynamics of decision-making and action during active sampling

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The dynamics of decision-making and action during active sampling

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ABSTRACT

Embodied Cognition Theories (ECTs) of decision-making propose that the decision process pervades the execution of choice actions and manifests itself in these actions. Decision-making scenarios where actions not only express the choice but also help sample information can provide a valuable, ecologically relevant model for this framework. We present a study to address this paradigmatic situation in humans. Subjects categorized (2AFC task) a central object image, blurred to different extents, by moving a cursor toward the left or right of the display. Upward cursor movements reduced the image blur and could be used to sample information. Thus, actions for decision and actions for sampling were orthogonal to each other. We analyzed response trajectories to test whether information-sampling movements co-occurred with the ongoing decision process. Trajectories were bimodally distributed, with one kind being direct towards one response option (non-sampling), and the other kind containing an initial upward component before veering off towards an option (sampling). This implies that there was an initial decision at the early stage of a trial, whether to sample information or not. Importantly, in sampling trials trajectories were not purely upward, but rather had a significant horizontal deviation early on. This result suggests that movements to sample information exhibit an online interaction with the decision process, therefore supporting the prediction of the ECTs under ecologically relevant constrains.

1. Introduction

The classical view of decision-making was founded on the idea that action is executed after a decision has been made, in a serial fashion (Newell & Simon, 1972, Pylyshyn, 1984). This idea assumes a temporal and functional separation between the decision-making processes and the ensuing motor processes that implement that decision. Recent behavioural studies have challenged this strictly serial view and proposed, instead, that the choice execution process may begin before the decision process has concluded, *de facto* introducing the parallel view of decision-making (Ghez, et. al., 1997, McKinstry, et. al., 2008). This parallel view states that there is an ongoing information flow from decision to action systems well before the decision process has been fully completed. According to this view, not only decision and action may coexist, but choice movements may be updated online based on newly acquired evidence (Coles, et. al., 1985).

To investigate the putative interaction between action and decision as it unfolds in time, some studies have used decision-making tasks which require continuous control of action. These tasks track responses executed on devices like joysticks, robotic handles, computer mice, or freely with hand reaching movements (Resulaj, et. la., 2009, Burk, et. al., 2014, Barca & Pezzulo, 2012, Song & Nakayama, 2008). Since these responses have a wide temporal and spatial span, they make it possible to study, and compare the movement dynamics during the decision-making process.

A typical finding that emerges from continuous movement paradigms when subjects must move toward one out of two alternative targets, is the prevalence of movement trajectories that are not perfectly direct to the chosen target (Song & Nakayama, 2008). These findings have shown that the initial phase of the response movement weighs in the paths to the two possible targets, maintaining a compromise which is later resolved by diversion of the trajectory committing to one of the targets (Chapman, et. al., 2010, Gallivan, et. al., 2011). Some scholars attributed these averaged movements to an error in movement planning or to uncertainty of the movement goals (Cisek, 2006, Haith, et. al., 2015). However, in decision making literature these averaged movement trajectories are commonly interpreted as a case of movement being planned and executed online during the decision process and more importantly, that there is a continuous crosstalk between these two processes (Cisek, Pastor-Bernier, 2014, Marcos, et. al., 2014). An exacerbated expression of this online crosstalk are changes of mind, trials in which the subject's response movement starts off toward one target but corrects on-the-fly toward the alternative target (Burk, et. al., 2014). In general, these findings motivated the parallel view of decision-making, which focuses on the ongoing one-way flow of information from decision to action.

Although the parallel view of decision-making assumes a richer interaction between action and decision than the strictly sequential view, it only accounts for the forward influence from decision to action. However, there is evidence for backward influence from action on decision as well. For example, Burk, and colleagues

(2014) showed that when the spatial distance between two response options is large, subjects make less changes of mind than when the distance between targets is shorter. This means that action costs are considered and influence the outcome of the decision process. In a similar vein, Cos and colleagues (2011) found that the amount of effort required to perform the response action biased performance in a decision-making task. There is, still, another type of backward influence from motor to decision processes: when actions help accrue information relevant for the decision. The present study addresses precisely this case.

We can frame the evidence mentioned above under Embodied Cognition Theories (ECT) of decision-making, whose common characteristic is the influence of action dynamics on decision as well as the influence of decision on action. Indeed, drawing connections between motor processes and decision-making has a conceptual grounding on the wider framework of sensorimotor and embodied views in cognitive sciences (Clark, 1999, O'Regan & Noe, 2001, Barsalou, 2008), a general conceptual shift that has pervaded recent views in decision-making. One clear example is Lepora & Pezzulo's Embodied Choice Model (2015). The model proposes a two-way online interaction between motor actions and decision processes and that this interaction allows for a fast update of movement and decision processes. A typical argument by example often used to support this view is that, in nature, animals must move about (their body and/or sensory epithelia) to be able to gather information that is relevant to making subsequent choices and planning upcoming actions (Lepora & Pezzulo, 2015). To use the information gained through movement though, there needs to be a backward flow of information from action-related motor processes to decision-making.

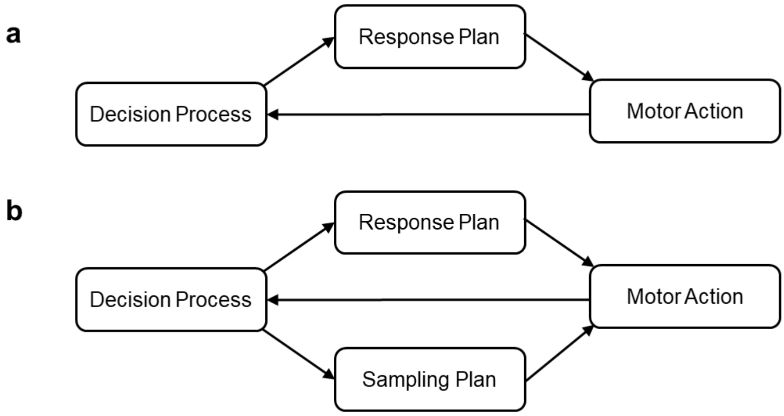

Figure 1. Interactions between motor action and decision in tasks without (**a**) and with (**b**) active information sampling. **a.** In majority of the decision-making tasks decision process feeds the response plan which gets executed with a motor action. While the action continues, the output of the action feeds back into the decision process. This is not a fully embodied scenario, since actions do not bring an information change**. b.** In a fully embodied scenario considered here, two different action plans, for sampling and for responding, are allowed to unfold in parallel. The decision process has a feedforward influence on motor output, whereas sampling influences decision via feedback from the motor action. In contrast to panel (**a**), the executed motor action implements both responding and sampling of information.

Despite the logical emphasis that embodied views make on information sampling movements, this notion has not been implemented in experimental tasks to support the ECTs. In fact, in most of these decision-making tasks, the stimulus information is available all at once and static, without any dependency upon the participant's movement (Lepora & Pezzulo, 2015, Barca & Pezzulo, 2012, Hudson, et. al., 2007, Marcos, et. al., 2013). The interactions which can be potentially at play in these types of tasks have been illustrated in Figure 1a. Because the actions performed to report a choice are inconsequential to the inflow of information used to reach that decision, these tasks cannot capture all possible interactions between action and decision proposed by ECTs. Therefore, there is a need for tasks that can reveal the two relevant aspects of actions to identify the potential interplay between motor and decision processes. This interplay, which has motivated the task used here to test decision-making under ECTs, is illustrated in Figure 1b. Here, we assume that there are two types of action plans which are critical in an embodied decision-making scenario, the ones necessary for response itself, and the ones necessary for information sampling. Both of them interact with the decision process, and mediate both feed-forward and feedback interactions.

In conclusion, we believe that the generality of the interplay between decision and action, and by proxy, of the embodied decision framework, have not yet been tested in all its critical components. In the present study, we aim to testing the ECTs' predictions with a task in which information accrual depends on the subject's actions. Empirical evidence regarding such a scenario is still scarce. We have developed a novel mouse-tracking task in which action is necessary both to sample information and to indicate the decision. To be able to single out one from the other, movements directed at sampling information and movements to execute the response have been made orthogonal. That is, it is possible for the subjects to accumulate all the information first and then make the choice, to make a choice at once without any accumulation of information, or to do anything in between. Since trials have a time limit, the orchestration among information sampling actions and choice actions becomes strategic. Although sampling and response actions have orthogonal axis, one critical aspect of the task is that both action plans are executed via the same effector, so that the final motor output must synthesise the two plans if they are to co-occur, as the theory predicts. Similar to other mouse-tracking studies, the main test of our hypothesis depended on the analysis of metrics obtained from the trajectories (Freeman, et. al., 2011).

Our hypothesis, derived from the ECTs (Lepora & Pezzulo, 2015, Cisek, Pastor-Bernier, 2014), is that the actions related to the decision-making process and the actions related to information sampling used to reach that decision are subject to significant online interaction. We first show that, in our task, trajectories depend on the amount of available information such that participants move to sample information when needed. Second, we demonstrate that the decision-making process transpires even at the initial phases of the information sampling movements, so that trajectories are biased towards one (usually the chosen) target much before all the information has been gathered. These results do not only suggest that the decision-making process pervades information sampling actions, but also that decision, actions and information sampling may be orchestrated in parallel, and not necessarily in a strictly sequential fashion.

2. Methods

2.1. Participants

Twenty-one voluntary participants joined the experiment (12 women, 9 men, average age 23.5 years). Participants were recruited from the database of the Center for Brain & Cognition (University Pompeu Fabra) and were paid 10 euros per hour in exchange for their participation. They were all right-handed and had normal or corrected to normal vision with no reported history of motor problems related to the upper limbs. Before proceeding with the experiment, all subjects read and signed an informed consent form. The research was conducted in accordance with the Declaration of Helsinki, institutional guidelines and regulations. The experimental protocol was approved by the ethics committee CEIC Parc de Salut Mar, Universitat Pompeu Fabra. Before conducting the hypothesis-driven data analyses, we excluded data from two subjects whose accuracy was below 75%. This ensured sufficient number of correct trials for obtaining reliable trajectory averages.

2.2. Experimental setup

Participants were asked to perform a visual object categorization between “edible” vs “non-edible” in a two-alternative forced choice (2AFC) paradigm. We used 63 edible and 63 non-edible object images from the Amsterdam Library of Object Images (Geusebroek, et. al., 2005), and each of them was presented only once to each participant, obtaining a total of 126 different trials per participant. To control for possible effects of colour cues, we used, achromatic versions of the images. Stimulus display and the task were programmed with MATLAB, PsychToolBox (Brainard, 1997). Visual stimuli were presented on a Cambridge Research Systems, Display++ monitor (1920 × 1080 pixels, 32'', 100 Hz refresh rate). Responses were recorded through a computer mouse (HP USB Optical Scroll Mouse), and the cursor location was recorded at 100 Hz (at every display refresh frame). The participant's task involved moving the cursor from a home position at the bottom centre of the display to the right or left response areas, depending on the choice regarding the image presented at the top centre (locations and other details are described below).

For each subject, the total of 126 trials were divided, randomly and equiprobably into three different movement-to-visibility conditions: No Blur (NB), Low Blur (LB) and High Blur (HB). In the NB condition, the images were fully visible (without any blur) from the beginning of the trial, and therefore visibility was not contingent on action. For the other two conditions, in order to implement movement-dependent updating of information, we manipulated the visibility of the object images as a function of mouse position. We used a dynamic filter mask over the image to blur the image. The filter convolved each pixel with the neighbouring pixels with a Gaussian kernel with standard deviation (sd) proportional to the vertical distance between current cursor position and the target image at the top centre of the display, denoted d_v (measured in pixels). In the LB condition, the Gaussian mask had sd = $d_v/120$, whereas in the HB condition the Gaussian mask had sd = $d_v/60$. This effectively made blur (hence, image visibility) depend on the participants' movement, so that moving upward de-blurred the target image (i.e., the shorter the vertical distance to target, the smaller d_v, and hence the lower the sd and the higher the visibility). The difference between the two blur conditions was the gain in visibility as a function of distance.

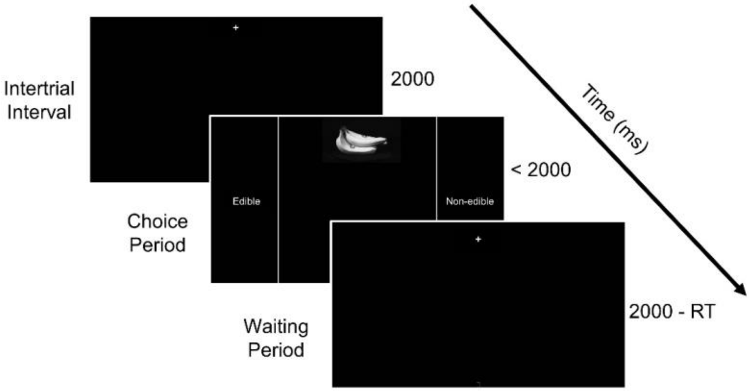

Figure 2. Schematic illustration of a trial sequence. Each trial was preceded by a 2000ms inter-trial interval displaying a fixation cross. Then, the stimulus and the choices were presented on the screen until response, with a deadline of 2000ms. Response areas, left and right of the display, are denoted by straight vertical lines. All trials were equated to the same duration, 2000ms by adding a waiting time if necessary. RT = reaction time.

2.3. Procedure

Each subject completed the task in a darkened, sound-attenuated laboratory room. Subjects completed a training session prior to the experimental block. The training consisted of 18 trials (6 from each blur condition in a random order) in which we used novel images that did not appear in the experiment. Before each trial started, the subject moved the mouse cursor to the bottom-centre home area (height = 10 x width = 15 pixels, centre x, y coordinates: 960,1075 pixels). The trial began with the image (265 x192 pixels) appearing at the top-centre of the monitor (x- coordinates: 827 to 1092, y-coordinates: 0 to 192 pixels). As soon as the image appeared, the subject was free to move the mouse to indicate her choice by reaching to, and clicking on, one of two response areas, left or right side of the display, within 2000 ms (Figure 2). The rectangular response areas, covering the leftmost and rightmost 23% of the display, were indicated by two vertical lines along the screen sides (x coordinates: 440 and 1480 pixels, respectively; see, Figure 2). For half of the participants, edible was attributed to the left response area and non-edible to the right. For the other half, it was reversed. Response deadline was 2000 ms, after which the subject missed the trial. The deadline was introduced to create time pressure. This and similar methodological practices to encourage early movement initiation are used commonly in mouse-tracking studies (Scherbaum & Kieslich, 2018, Fischer & Hartmann, 2014). In our particular protocol, this deadline had been established after previous pilots, and rendered average performance below ceiling but within the pre-set subject inclusion criteria (<75 %). As it will become clear later, the trial time imposed could be (and was) used up in different ways depending on the available information at the beginning of the trial (see *Movement onset latency analysis* in the Results section). Each trial took the whole 2000 ms, independently of the response time, to ensure that the duration of the session was fixed. After a trial ended, the participant needed to move the cursor back to the bottom-centre home location for the next trial to begin. The inter-trial interval was 2000 ms, which also served as a fixation screen. Trials from all three conditions (NB, LB, HB) were interleaved randomly throughout the experiment. Hence, for efficient responding, participants could not fall back on a pre-defined strategy based on visibility prior to the start of the trial.

Because the response areas covered both lateral sides of the display, the decision movement could vary in terms of the vertical extent of the trajectory, including direct horizontal movements from the home location to the response area. As said earlier, in the blurred image (LB and HB) conditions, the image blur decreased as the mouse moved upward. Therefore, when the image did not contain sufficient information, the participant needed to move in the vertical direction in order to gather evidence. Because of the response deadline (2000 ms), moving upward had a cost (i.e., took time off the available response time). Therefore, moving upward is not an optimal strategy if it is not necessary to sample evidence.

2.4. Data Analysis

In our task, characterizing information sampling and response components of the subjects' action boils down to the analysis of heights and angles of the response trajectories (some example trajectories are shown in Figure 3). Firstly, we inspected the trajectory height, denoted h, which was calculated by measuring the vertical distance (in pixels) between the starting point and the highest point of the trajectory (Figure 3a). Second, we analysed the initial angle of trajectories, denoted α, which was defined as the angle described by an imaginary straight line connecting the starting point with the point at one-third of the length of the trajectory (cyan dashed line in Figure 3a), with respect to the vertical midline (0º). It is important to note that, although correct targets were randomly assigned left or right sides during the task, for analyses we realigned the correct choice to positive angles. Henceforth, positive angles indicate the direction of the correct choice, and negative angles that of the incorrect choice. Despite we excluded incorrect trials from the analysis, negative angles are possible at initial stages in the trajectory of correct trials.

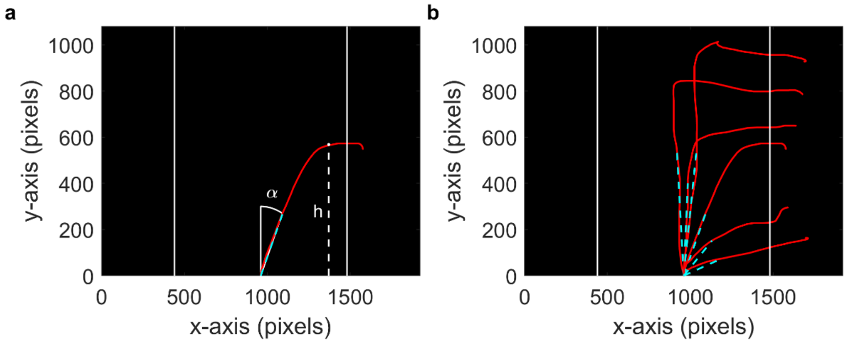

Figure 3. a. An example of one mouse trajectory (red line) on the experimental display. Response areas are indicated to the participants by the solid vertical lines on the left and right sides. The white dashed line indicates the height *h* of the trajectory. The cyan dashed line that joints the origin with the point of the trajectory that lies at one third of its total length serves to calculate the initial angle α of the trajectory with respect to vertical. Positive angles are defined to be in the direction of the correct target, whose location could occur randomly on either side. **b.** Examples of trajectories for several individual trials, with the same conventions described in a.

We preregistered this study and we first report the analyses that were planned prior to data collection (see, https://osf.io/3ysah/). We also performed follow-up analyses that have been decided after the pre-registration process, as these reveal important characteristics of the data. Throughout the results section we report statistical tests according to the frequentist approach (the analogous Bayesian analyses are reported in the Supplementary Table S1, as both analyses lead to the same conclusions). We excluded incorrect trials from the trajectory analyses, as is usual practice in order to extract decision-related effects from categorically similar responses (Barca & Pezzulo, 2015, Quinton, et. al., 2013, Flumini, et. al., 2015). On average, each participant had 110 correct trials (range103 – 123) out of 126 total (overall mean accuracy >87%). The mean number correct trials out of 42 per condition was 37.4 (sd = 3.6), 36.9 (sd = 2.7) and 36.2 (sd = 2.8) for NB, LB and HB conditions, respectively. This indicates that the increase in blur ended up with slightly lower accuracy rates. The mean response time of correct trials was 1107 ms (sd = 117), 1266 ms (sd = 135) and 1374 ms (sd = 142) for NB, LB and HB conditions, respectively. The increase in blur resulted in longer response times in addition to lower accuracy.

3. Results

3.1. Movement-dependent information sampling

If participants gather information as is needed, their trajectories should reach higher when the image is blurred. We therefore tested whether trajectories in blur trials reached higher than trajectories in the no blur trials. As can be seen in Figure 4a, trajectories in the two blur conditions were higher than in the no blur condition, since information sampling was unnecessary in the latter (right tail paired-samples t-tests, t(17) = 6.53, p < 0.001, Cohen’s d = 1.54;

t(17) = 7.03, $p < 0.001$, Cohen's d = 1.66, for the comparison of NB with LB and HB, respectively). This result rules out the option that participants used a good-for-all strategy, by just moving up as soon as the trial started and then deciding which side to go. However, even in the NB conditions trajectories had a non-zero vertical component (mean = 368.3 pixels, sd = 231.9), possibly due to biophysical motor constraints. Another potential reason for non-zero height in NB condition is the random presentation of conditions in the experiment. Since in approximately two thirds of the trials gathering more information has an advantage, participants might have an anticipatory tendency to move upwards. To eliminate the height differences that are present in the trajectories but unrelated to information gathering, we subtracted the average height in NB condition from LB and HB trajectory heights in each individual's data and continued the analysis with these normalized values. The results showed that trajectories in HB trials were about 27% higher than in LB trials (mean = 315.7, sd = 190.4, vs 229.3, sd = 148.8, respectively; right tail paired-samples t-test, t(17) = 5.39, $p < 0.001$, Cohen's d = 1.27).

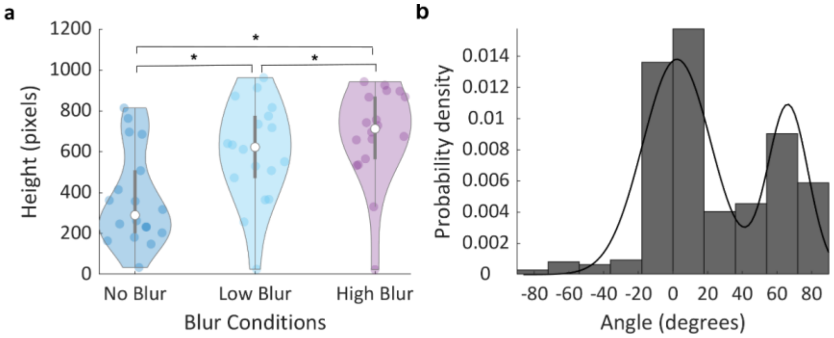

Figure 4.a. Height of trial trajectories for NB, LB and HB conditions. Each colored dot represents individual means for the corresponding condition. White dots represent the group median for the condition and the grey lines represent the inter-quartile range. **b.** Probability density of the initial angles of the trajectories across participants. The solid black line corresponds to the Gaussian mixture model (with 2 components) fit to the distribution (model with 2 components AIC = 19105 < model with 1 component AIC = 19753). Angle 0º corresponds to straight vertical upwards movement, i.e., with no horizontal component. Positive angles correspond to correct target direction.

3.2. Interplay between decision and action

Bimodality of trajectories. A central prediction of ECTs is that movements should reflect the decision-making process throughout, such that the trajectories should show early on a bias towards the finally chosen target. We tested this prediction by studying the initial angles of the trajectories (Figure 4b). However, for this analysis we decided to include only those trials for which sampling had occurred, instead of mixing in trials with and without sampling behaviour. This was motivated by the fact that the distribution of angles was clearly bimodal (Hartigan's Dip Test (Hartigan & Hartigan, 1985), p-value < 0.001; Gaussian mixture model better fit with 2 components, Akaike Information Criterion (AIC) = 19105 than the model with 1 component, AIC = 19753). A central lobe of the distribution peaked at an angle 2.3° (that is, close to vertical, which was arbitrarily defined to be 0°), and a lateral lobe peaked at 66.4° (positive angles correspond to directions to the correct target, with 90° being a perfectly straight trajectory). The separation between the two lobes of the bimodal distribution was therefore 43.52 °. Detecting subtypes of trajectories is fundamental to avoid averaging trials that are different in terms of the underlying cognitive modes (Hehman, et. al., 2015, Wulff, et. al., 2019). Please, note that in our case averaging these two types of trajectories could end up rendering an average trajectory between sampling and non-sampling that is unrepresentative of the majority of the responses, which are of one or the other kind. Therefore, this bimodality and the cut-off point allowed us to classify trajectories as sampling or non-sampling, depending on whether the initial angle is closer to the central or the lateral peak of the bimodal distribution, respectively. Apart from the bimodality at group level, we confirmed significant bimodality in the distribution of trajectory angles for each subject individually (see Figure S1) for 9 out of 18 subjects. This means that early on in a trial, there is a fast sub-decision regarding the sampling or non-sampling strategy. This is further supported by the movement onset latency results, below.

The presence of two types of trajectories can be observed in each blur condition separately (Figure S2). As one would expect, there is a large fraction of non-sampling trajectories in the NB condition (corresponding to the lateral lobe of the bimodal distribution; q = 0.62, $X^2(1, N = 635) = 39.86$, $p < 0.001$), though perhaps surprisingly in the HB condition there was a fraction of non-sampling trajectories ($q = 0.14$ binomial test $p < .05$). The presence of sampling and non-sampling trajectories across all blur conditions suggests that participants made an initial choice about whether or not to gather information. This is supported by an analysis that showed that trajectories classified as non-sampling had a much smaller height than sampling trajectories (right tail two-sample t-test, $t(17) = 11.9$, $p < .001$). Thus, non-sampling trajectories simply reflect a direct movement towards the chosen target that emanates from an initial decision, with little information gathering or ongoing decision-process throughout.

Movement onset latency analysis. We estimated the latency of movement onset as the time between trial onset and the initial movement of the mouse. The analysis showed that mean latency in non-sampling trials was longer (mean = 435 ms, sd = 125 ms) compared to sampling trials (mean = 329 ms, sd = 77 ms; right tail two-sample t-test, $t(17) = -4.4$, $p < .001$, Cohen's $d = -1.04$). This means that when the subjects exhibited a non-sampling strategy, they generally did so after waiting for longer at the initial location. This adds support to the interpretation that there is an initial sub-decision about whether to sample information or not, happening early in the trial, based on the available information about the target.

Speed of movement analysis. We estimated the average speed of trajectories in each condition. The mean speed was higher in HB (mean = 30.2 cm/s, sd = 6.9) and LB (mean = 28.8 cm/s, sd = 7.6) compared to NB (mean = 23 .9 cm/s, sd = 7.5) condition. We conducted repeated measures ANOVA to see the effect of blur on movement speed. The results showed that movement speed was significantly modulated by blur ($F(2,34) = 37.2$, $p < 0.001$, $\eta^2 = .68$)

Angle analysis of sampling trajectories. Thus, given the initial sub-decision and the ensuing existence of two different types of trajectories, a direct test of the prediction of ECT requires examining the sampling trajectories alone. These trajectories correspond to the central peak of the distribution in Fig. 4b. As the initial angles of these trials are close to zero (vertical), trajectories mostly depart vertically from the home position with the aim of gathering information to guide the final choice. However, a key finding is that in addition to the prominent vertical component, the initial steps of the trajectory were already biased towards the chosen target, as the initial angle was significantly larger than zero in both LB and HB conditions (right tail one sample t-tests, $t(16) = 4.58$, $p < .001$ and $t(16) = 3.41$, $p = .002$, respectively). This result strongly supports the notion that the decision process transpires into the movement even whilst participants are actively sampling information.

One might argue that some trials in the analysis above might have been misclassified (as non-sampling, instead of sampling trials), given the partial overlap of the two lobes of the bimodal distribution of angles. This could introduce some biases towards positive angles. To control for this possible confound we used a more data-driven analysis limited to LB and HB trials only (in which participants are, for the most part, in need to sample information), that does not rely on trial classification. In this analysis we calculated average angle in incremental ranges of angles (symmetric around 0º) from ±1º to ±30º, in steps of one degree (Figure 5a). We found that the average angle was significantly larger than zero in all the ranges larger than ±14º (right tail t-tests, $p < .05$, see Figure 5a). Angles in the range ±14º and ±20º are well inside the central peak of the bimodal distribution, as described above, and therefore can be independently classified as sampling trajectories (trajectories with such small initial angle very unlikely correspond to trials where the decision maker already made a choice about where to move). In sum, this new analysis reveals that trajectories whose initial angles lie within a small range of angles symmetrical around zero already show a significant bias towards the chosen target. This result supports, once more, the notion that the ongoing decision-making process transpires into the movement well before all the information necessary to solve the task has been gathered.

Although we did find significant deviations in the initial angle of blur trials (HB, LB) we did observe only marginal evidence that the angle deviation was larger in LB (mean = 5.28º, sd = 4.75) than in HB (mean = 3.42º, sd = 4.13) conditions (Fig. 5b; right tail paired-samples t-test, $t(16) = 1.66$, $p = 0.058$, Cohen's $d = .4$).

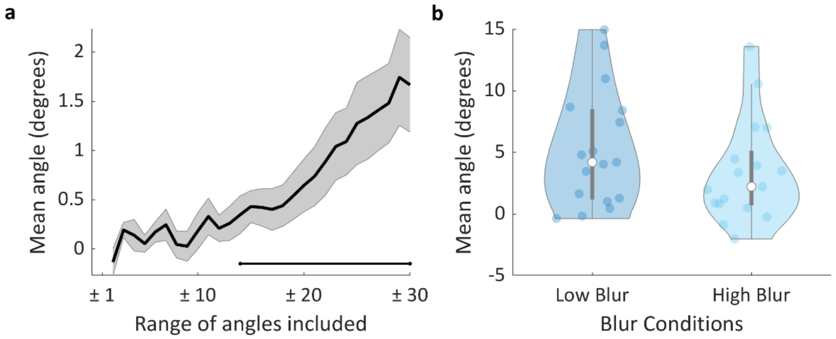

Figure 5. a. Mean initial trajectory angle for all blur trajectories (pooled LB and HB data), along incremental ranges of angles symmetric around zero. The solid black line corresponds to the inter-individual mean (the grey area represents s.e.m.). The black horizontal line represents significance (right tail t-test, $p < 0.05$) against the hypothesis that the mean angle is not larger than zero. **b.** Initial angle of trial trajectories for LB and HB conditions. The coloured dots represent each participant's mean value for the corresponding condition. The white dots represent the median for each condition and the grey lines illustrate the inter-quartile range.

3.3. Converging evidence from angle and height information

Initially we had decided to classify sampling and non-sampling trials based on initial angle of the trajectories. However, if our hypothesis is correct, a similar classification should apply to the heights of the trajectories. This is because sampling trajectories are expected to reach higher than non-sampling trajectories, as the latter correspond to ballistic movements to the target without much ongoing deliberations and thus are expected to reach vertically much lower. What is more, if trajectories are truly separable into sampling and non-sampling, then it should be the case that in their heights should also be distributed in a bimodal way, and height and angle should be correlated. Consistent with this prediction, we found that heights were distributed in bimodally (Figure 6a) across conditions and participants (Figure 6a; Hartigan's Dip Test, $p < 0.05$; see Figure S3 for each blur condition). These results in turn suggest that it should be possible to classify trajectories as sampling and non-sampling based on the bimodality in heights, and that this classification should be largely consistent with the one derived above from the angle analyses. In line with this, classification based on height and classification based on angle were highly correlated (Pearson's correlation, $r = 0.76$) and clustered trials in two clear categories (Figure 6b).

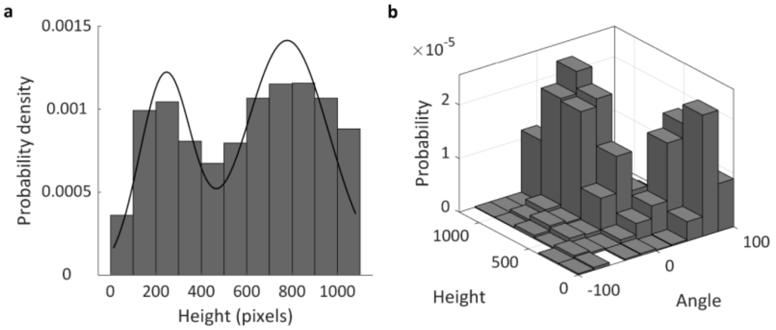

Figure 6. a. Probability density of the heights of the trajectories across participants. The solid black line corresponds to the Gaussian mixture model with 2 components fit to the distribution (better fit in the model with 2 components, AIC = 26439 lower than the model with 1 component, AIC = 26874). **b.** Probability density of the heights and angles of the trajectories across participants.

Similar to the main angle analysis reported in Section 3.2 (where trial classification was based on angle), we analysed angle again but this time using trial classification based on height. We found that the angles in sampling trials, both the LB and the HB conditions, were significantly larger than zero (right tail one sample t-test, $t(16) = 3.7$, $p < 0.001$, Cohen's $d = .9$ and $t(16) = 2.05$, $p = 0.029$, $d = .5$, respectively). This outcome corroborates the conclusions of our main analysis and shows that this finding generalizes regardless of the classification variable used.

3.4. Generalization of the results along the trajectory

In the main analysis, we estimated angles at one third of the trajectory, as we wanted to capture the initial moments of the response movement. However, the criterion to compute angles at one-third of the trajectory is somehow arbitrary. As a check regarding the reliability of this result, and the validity of the criterion used, we decided to compute the angles along the whole trajectory at 10 equidistant points, from 1/10th to 10/10th of the trajectory length. Then we checked the distribution of angles at each of these trajectory points. We found significant bimodality of angle distributions in all except the last trajectory point (Hartigan's Dip test, $p < 0.05$). This generalizes the bimodality of trajectories beyond the one particular point used in the main analysis. As can be seen in Figure 7, the distribution of angles from 1/10th to 5/10th of trajectory shows an earlier peak closer to 0° which means that a portion of trials classified as sampling are still in a phase of upward movement. Logically, at later stages the trajectories show diversion towards the final choice. Therefore, we are safe to interpret our main results obtained from angles calculated at the 1/3rd of the trajectory length as it is early enough to check if decision transpires into the movement during active sampling.

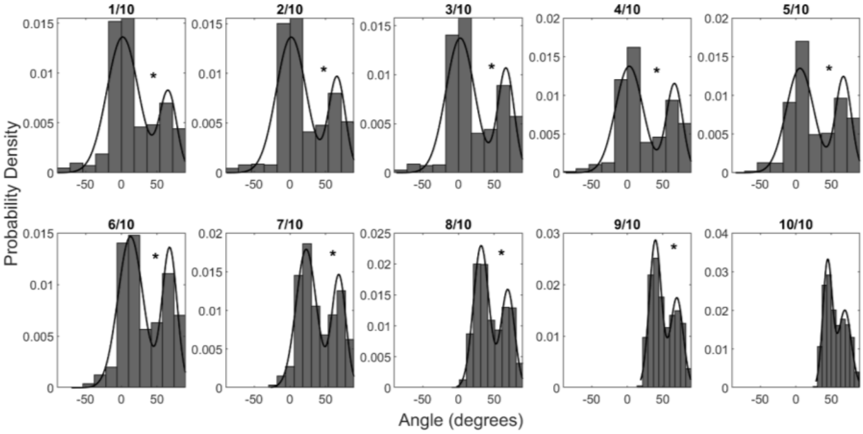

Figure 7. Probability density of angles calculated at 1/10th to 10/10th of trajectory length. The solid black lines correspond to the Gaussian mixture model with 2 components fit to the distribution. The asterisks indicate the significance of Hartigan's dip test for bimodality ($p < 0.05$).

3.5. Angle and height analyses including error trials

It is common practice to use only correct trials in trajectory analyses (Barca & Pezzulo, 2015, Quinton, et. al., 2013, Flumini, et. al., 2015), because the aetiology of errors is varied and difficult to trace. However, one could argue that removing error trials might have biased the outcomes toward positive angles. In order to ensure that the results we found were not due to biases induced by the exclusion of error trials, we repeated the height and angle analysis, this time including error trials along with the correct trials. We found that NB trials (mean = 393.6, sd = 208) had significantly lower height than LB (mean = 636.6, sd = 185.7) and HB (mean = 726.8, sd = 150.8) conditions (right tail paired-samples t-tests, $t(17) = 7.6$, $p < .001$ and $t(17) = 8.1$, $p < .001$, respectively). As in the main Results section 3.2, we subtracted the NB average height from

LB and HB and compared them. The result of the right tail paired-samples t-test showed that HB trajectories were significantly higher than LB trajectories (t(17) = 5.2, p < .001) , confirming the main results conducted only on correct responses. Similarly, we assessed the angle of sampling trajectories in LB (mean = 4.6, sd = 4.2) and HB (mean = 2.1, sd = 3.9) and found that both were significantly above 0 (right tail one sample t-tests, t(17) =.4.7, p < .001 and t(17) = 2.3, p < .05, respectively). We conducted right tail paired-sample t-test, to test if LB had larger angles than HB. The results showed that LB had significantly larger angles than HB (t(17) = 2.5, p < .01). Thus, we can conclude that the results we reported were not biased due to exclusion of error trials. As we see that the direction and significance of the effects did not change when the analysis were repeated with correct and incorrect trials altogether.

4. Discussion

Many studies in the past have challenged the classical view of decision-making and cognition which assumes a temporal and functional separation between decision and action systems (Newell & Simon, 1972, Pylyshyn, 1984). The newer view is that natural choice actions in humans and other animals involve movement patterns that reflect, in part, the ongoing decision process. As a result, movement trajectory analyses in continuous control tasks have been increasingly used to trace the underlying decision dynamics. The outcome of the present study clearly sides with this framework, showing that it is possible to trace decision dynamics from the ongoing choice action (Tabor, et. al., 1997, Magnuson, 2005, Spivey & Dale, 2006). However, the majority of the tasks used in previous studies did not contemplate decision-making scenarios where actions are also required to sample information. This scenario characterises choice in many natural environments, such as getting closer to an object to decide whether it is nutritious food or else should be avoided. To fill this gap in the literature, we tested whether the outcome of decision processes pervades sampling actions.

As mentioned in the introduction, parallel processing of decision-making and action control processes is an important principle. However, the nature of the interaction between the two is still under debate, given that a strictly parallel view might be insufficient to account for the full range of decision and action interactions. For instance, Lepora and Pezzulo (2015) have put forward the ‘embodied choice’ framework, that accommodates richer interactions between action and decision through action-dependent information gain, compared to the parallel account. However, the experimental tasks they have used to illustrate their predictions lacked the active sampling component, which leaves one main prediction of the theory still unresolved. The findings of the current study support the ‘embodied choice’ theory by showing that the interaction between decision and action can be revealed, and traced in the decision responses, under ecological scenarios that incorporate the active sampling constrain. If this were not the case, we would have observed a temporally separated sampling and responding characteristics in the movement trajectory without any angular deviation during sampling, in early parts of the trajectories.

In fact, that non-sampling trajectories observed in our data revealed a kind of serial decision-making pattern which consists of a longer stationary period followed by a shorter movement (Results section, movement onset analysis). However, sampling trajectories were characterized by moving earlier (shorter stationary period) followed by a longer movement directed at sampling which is biased by the decision process. Thus, rather than claiming that all decisions are fully parallel and continuous, our preferred interpretation is that, even if there are certain stages in the decision process, some of them allow for continuous interaction of action and decision status.

One central feature of the task used in the present study is that participants must trade off information (image de-blurring) for energetic efficiency (moving up, hence orthogonal to the choice goal). This is because motor execution involves expenditure of energy, thus incurring effort-related costs. Motor cost and physical effort have started to be studied in relation to decision-making (Burk, et. al., 2014, Marcos, et. al., 2015). For instance, Cos and colleagues (2014) have shown that effort and biomechanics of a task influence the decision dynamics starting at early stages. It is likely that physical effort influences the decision dynamics due to the strong interactions between action and decision. In our experiment, each blur condition had a different cost/information structure. Although, it is not easy to quantify exactly how this effort-to-information ratio impacted our results (due to the use of real images instead of parametric stimuli), it is still safe to say that the effort associated to information sampling altered the decision-making process, rendering differences in choice trajectories. The analyses showing an inverse relationship between image visibility and trajectory height clearly support this.

The main result to emerge from this study, however, was based on the deviations and curvatures in choice trajectories. Please note that this is only superficially similar to other mouse-tracking studies (Spivey, et. al., 2010, Freeman, 2018, Wojnowicz, et. al., 2009). A common task characteristic our current study shares with this previous work is the urgency of responding (Scherbaum & Kieslich, 2018, Kieslich, et. al., 2019). Via imposing time pressure, participants are encouraged to execute decision and action in the same time window as it is more optimal for a successful response than staying stationary to make a decision and then move to report it. However, the fundamental feature of our experiment compared to others in the decision-making literature is the presence of a functional link between information and movement. In those previous works, the subject planned and performed actions to report the choice response, therefore effectively allowing to study interactions between decision process and response plan only in one direction (as shown in Figure 1a). In contrast, the task we developed here involves, and makes it possible to study, both response and sampling plans and their mutual interplay (Figure 1b). Another way to put it is that most of the previous studies so far have considered only tasks equivalent to the ‘no blur’ condition of our study. Hence, one of the main goals here was to compare the trajectories between different sampling conditions as a function of movement-to-information ratio. First, the results obtained conclusively support the prediction that the decision process pervades information sampling movements in various ways. Information sampling trajectories deviated toward one of the choices (the correct one, on average) very early on. We confirmed this both in low blur and high blur conditions, using only trials classified as sampling trials. A second expectation by hypothesis was that, if the sampling component was stronger in high versus low blur conditions, then one would assume that the decision component will be more pronounced in the trajectories of low blur trials than in those of high blur trials, especially at early stages. This is because the need for information in high blur trials is stronger. Angular differences between low and high blur conditions calculated according to the planned analysis (at 1/3th of trajectories) were in the expected direction, but reached only a marginally significant effect. This borderline result may be due to the fact that the two conditions were not sufficiently different in terms of costs of sampling movement (effort-to-information ratio). This cost depended directly on the blur function, which was chosen arbitrarily. Indeed, subsequent analyses where angle was calculated at different stages throughout trajectories, or when angular deviation was calculated in incremental steps from movement origin, revealed robust significant differences in the same, predicted direction. This variability reflects the importance of the task mechanics to the study of sensorimotor interactions in a decision-making setting (Kieslich, et. al., 2019). Variants of active sampling decision-making tasks, including variations of the information cost function, should shed more light on the full range of embodied decisions under naturalistic constrains.

We argue that the proposed interactions between action and decision revealed by our data rely on the incorporation of sampling and responding actions in the task structure (as illustrated in Figure 1b). We note that the tasks that include movement-agnostic stimulus, often used in the literature (and illustrated in Figure 1a), are a special instance of the more general case modelled in Figure 1b: one in which the arrows to and from "sampling plan" have zero weight. This is also the case of non-sampling trajectories that we observed in our study. Yet, our experimental setup is not intended as a general model for all action-decision possibilities that humans and animals are capable of. We rather claim that embodied decisions are the manifestation of the flexibility of the decision process (Wispinski, et. al., 2018). In many natural and ecological situations, like the one modelled here, decisions have to be carried out as ECTs predict –with a strong interaction coupling with action processes. Nevertheless, there are also abstract and higher-level decisions which may comply with serial accounts of decision-making, especially in humans given their more sophisticated planning strategies. In line with a 'phylogenetic refinement' view, fully abstract cognitive operations are evolutionarily more recent, whereas rich cycles of action and decision are prevalent from very basic animals to complex mammals (Cisek, 2019). In the human context, depending on the task, the biomechanical characteristics and previous experience, we may observe response patterns ranging from a pure abstract and covert decision-making process that precedes any action, to a fully embodied and interactive one such as the one seen here. For instance, a novice driver may find herself thinking step-by-step about all of the driving actions before executing them, however as practice accumulates, she may decide and move at the same time with ease. Therefore, we are aware of the vast complexity underlying the interaction between decision and motor action (Gallivan, et. al., 2018). Previous studies have succeeded in revealing the impact of decisions on choice actions in situations where actions do not contribute information. Our study provides one step forward in understanding these interactions under the new constrain of action-dependent information sampling. What we have shown is that when the task dynamics imposes this type of ecological constraint, action for sampling and choice action have interactions with the decision process and with each other.

Despite the novelty of the present study, it has covered only a subset of situations and some areas of the decision-action process remain uncharted. For instance, in this study we used orthogonal vertical and horizontal movement components to observe sampling and decision respectively. Yet, the weights of these movement axes are not equal, considering the display dimensions and the difficulty of equating a level of information gained with a unit of sampling movement and a level of decision criterion with a unit of response movement. In the future, different approaches such as reward structures and/or stimulus that allow parametric information gain can be utilized to answer more specific questions about action and decision interaction. Besides the task design aspects, we are not oblivious to the fact that the present group patterns on which we have based our conclusions contain important individual differences. These individual patterns may reveal fundamentally different strategies in the trade-off between information sampling and decision. Uncovering the hidden dynamics behind them will be key to characterize embodied decisions. Lastly, in this study we have focused our analysis on the correct trials and therefore designed a task with a ceiling level performance. In decision-making field, error responses are crucial to understand the underlying mechanisms. After establishing the main principles of the ECTs, we expect to see studies delving on to error behaviours and enriching our understanding of embodied decisions.

To summarize, the present study provides a demonstration of interactions between action to sample information, action to respond, and decision process with a novel mouse-tracking task. Our results show that decision outcomes feed into movement trajectory during information sampling movements which, in turn, accrue decision-relevant information. This is a support for the embodied theories in decision-making with a task that allows to inspect rich action-dependent sampling mechanisms.

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Supplementary Information

1. Supplementary Figures

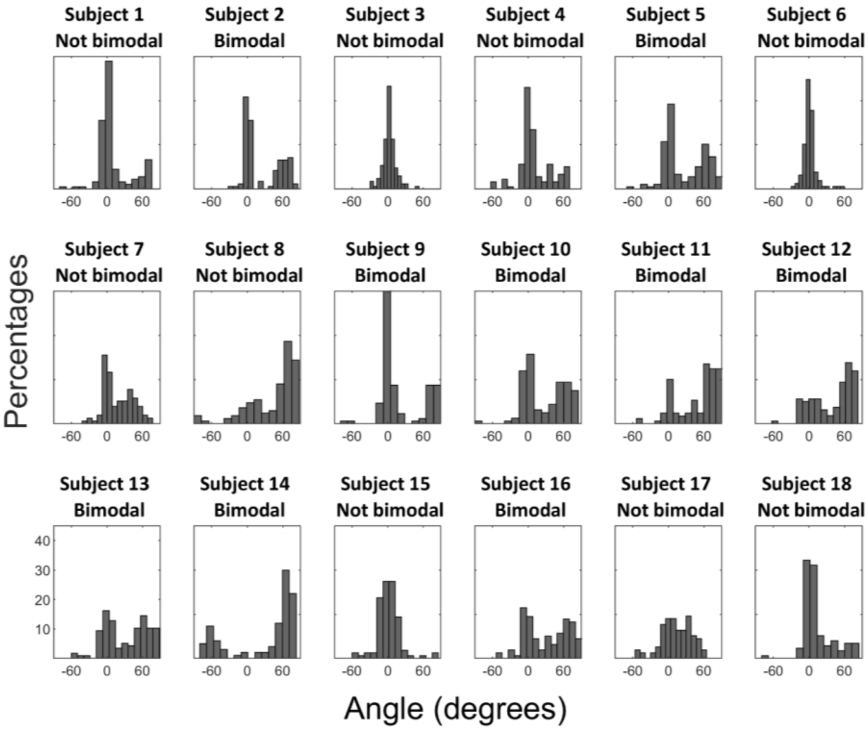

Figure S1. Distribution of angles for each individual subject.

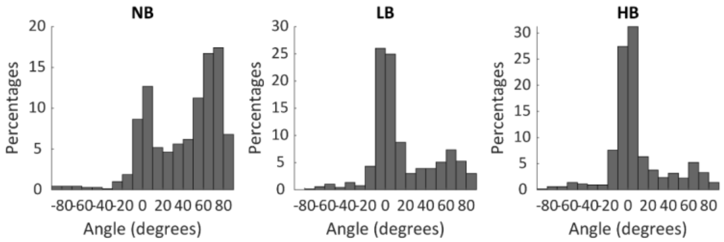

Figure S2. Distribution of trajectory angles for each blur condition

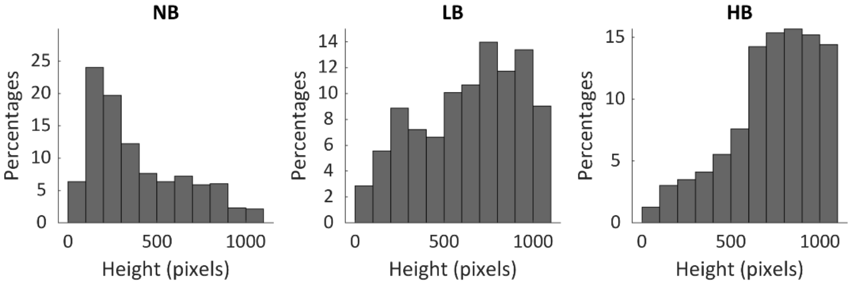

Figure S3. Distribution of trajectory heights across participants for each blur condition.

2. Supplementary Table

	Page	Analysis Variable	H1	Bayes Factor	Error	Median Effect Size	95% CI	Frequentist p-values
1	7	Height (all trials)	HB > LB	1067.6	< 0.001	1.17	[0.54, 1.79]	<0.001
2	9	Angle (classification based on angle)	LB > 0	209.53	<0.001	1.01	[0.41, 1.63]	<0.001
3	9	Angle (classification based on angle)	HB > 0	25.27	<0.001	0.73	[0.21, 1.29]	=0.002
4	10	Angle (classification based on angle)	LB > HB	1.45	0.004	0.37	[0.04, 1.12]	=0.058
5	11	Angle (classification based on height)	LB > 0	44.02	<0.001	0.8	[0.26, 1.38]	<0.001
6	11	Angle (classification based on height)	HB > 0	2.56	0.002	0.44	[0.06, 0.93]	=0.029

Table S1. Bayesian counterparts of the t-tests that have been reported in the Results section. The analyses are ranked in the order of appearing in text.

2.2. Physical effort contributes to speed-accuracy trade-off and urgency in decision-making

Ozbagci, D., Cos, I., Soto-Faraco, S., Moreno-Bote, R.

Physical effort contributes to speed-accuracy trade-off and urgency in decision-making

In preparation

Physical effort contributes to speed-accuracy trade-off and urgency in decision-making

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ABSTRACT

When making decisions one must consider the costs of gathering relevant information. It is well known that time imposes a cost expressed through the urgency to execute the choice. However, other potential costs contributing to urgency, such as the physical effort necessary to gather evidence, have been largely overlooked. Here, we address the hypothesis that physical effort used to gather evidence can alter decision-making dynamics by modulating urgency. To test this, we used a random dot motion discrimination task where stimulus viewing was contingent upon continuous effort exertion on a dynamometer. By manipulating the amount of physical effort of the hand press and the response deadline, we addressed whether effort induced speed-accuracy trade-off changes similar to those of deadline manipulations. The results showed that physical effort speeded up RTs similar to a deadline curtail, and reduced accuracy and motion discrimination performance. Overall, we propose that physical effort as well as time pressure costs converge as the decision process unfolds, and tax the decision maker with an urgency signal that accumulates in time.

1. Introduction

Quite often we must make decisions in the face of time constrains and limited resources available to gather information (e.g., physical and/or cognitive effort). In many ecological situations, accumulating information and making subsequent decisions is contingent on both effort and time pressure involved in the task. For instance, riding a bike in a city requires the orchestration of fast decisions and effortful actions like pedaling and braking, within hard time constraints like complying with street lights, making turns etc. This implies solving an optimality problem by considering time and effort as currencies toward obtaining outcomes. Sometimes it may be more attractive to make an early decision with less effort even at the cost of reduced accuracy, whereas in other contexts greater amounts of effort may be invested to secure precision on a certain outcome. This is the notion of speed accuracy trade-off (SAT), and many influential decision-making models in neuroscience and economy have tried to account for its underlying mechanisms (Wald, 1947, Edwards, 1965, Ratcliff & Rouder, 1998). However, while time constraints and SAT have received a wide attention in the study of decision-making, physical effort and its potential effects on decisions have been mostly neglected until the last couple of decades (Kurniawan, et.al., 2011, Cos, 2017, Dounskaia, 2010, Cos, et. al., 2014, Cos, et.al., 2011). This is remarkable, given that the putative importance that physical effort has as a constraining resource for behavior. In the present study we address the impact of the physical effort used to control accumulation of information on decision-making, and draw comparisons to the known effects of time constraints. We will consider previous findings on time constraints in relation to decisions, their interaction with the motor system, and common mechanisms that might drive both time-related and effort-related effects.

Accumulation-to-threshold models posit decision as a process of accumulation of evidence until a bound is reached. According to these models, SAT may be generally explained by a positive relationship between, on average, longer evidence accumulation (with greater gains in evidence) and higher accuracy (Heitz, 2019). This even happens in difficult trials where sensory information is noisy and the trial condition is difficult: the longer the accumulated evidence, the higher the accuracy (Shadlen & Kiani, 2013). However, in difficult trials the gain in accuracy obtained by observing longer the stimulus might not pay off the protracted observation time. To optimally solve this tradeoff, the decision process is additionally endowed with an urgency signal that tracks the passage of time, and pushes the decision process to terminate even if the evidence is noisy (Drugowitsch, et. al., 2012, Thura, et. al. 2014). There are two ways in which the urgency signal can be incorporated into the current models of decision-making. The first is collapsing decision bounds as a function of time, effectively triggering response in later stages of the deliberation with less evidence accumulated (Drugowitsch, et. al., 2012). The second is a signal that multiplies the accumulated evidence and increases as the accumulation continues. Both implement a signal that facilitate reaching a decision as time goes by, at the cost of lesser certainty (Thura, et. al. 2014).

Due to the conceptual connection between urgency and SAT, urgency is studied through task manipulations known to affect SAT. For instance, emphasizing speed or accuracy in a reaction time task, or manipulating trial deadline (Heitz, 2019). This approach is also used to address the brain correlates of the putative urgency signal. Neurophysiological recordings have pointed out the neural signals related to motor processing for carrying out urgency-related brain activity. For instance, when response speed was emphasized in a decision-making task, Spieser and colleagues (2017) found that the interval between EMG (electromyographic) activity onset and the behavioral response was reduced, showing a modulation in the motor system which operates fast movements in speeded decision-making tasks. There is also evidence for higher motor preparation (indexed by a decrease in in mu/beta-band oscillations in scalp EEG) over the motor cortex prior to stimulus under time pressure (Steinemann, et. al., 2018). This indicates that the context-dependent urgency (speed or accuracy emphasis) regulates the baseline activity in the motor pathway. In keeping with this, an electrophysiological study by Thura & Cisek (2014) found activity in primary motor cortex and premotor cortex of monkeys that reflects both the accumulated sensory evidence but also the animals’ subjective urgency to act. Altogether, this evidence strongly suggests that the urgency signal has significant impact on preparatory motor activity, as well as implications for motor execution of responses.

It is plausible to think of urgency in terms of time cost. When a decision has to be made rapidly, time has a higher cost, and therefore it is traded off with a heightened activation in the motor system (Standage, et. al., 2014). This can explain the baseline adjustment of motor preparation in speeded tasks mentioned in the previous paragraph (Steinemann, et. al., 2018). Given the close connection between urgency and motor processes, researchers have wondered whether urgency is implemented through striatal networks responsible for reward/cost mechanisms and motivated behavior (i.e., basal ganglia) (Carland et. al., 2019). Since basal ganglia activity predicts rewards and modulates the speed of movements (Houk, et. al., 1995 & Schultz & Romo 1992), it is a candidate structure for aiding SAT-related changes in motor processing. Supporting this logic, research has actually shown that the basal ganglia exhibited SAT related modulations (Bogacz, et. al., 2010, Forstmann, et. al., 2010, van Maanen, 2016). For example, van Maanen (2016) showed that the striatum showed higher activation when the participants had a stronger urgency to respond. Taken together, in addition to leading to motor excitability, urgency can be seen as a mechanism to balance rewards and costs within the task at hand, through the striatal network.

Despite the studies discussed so far implemented urgency in the form of time cost, it is important to bear in mind that decision-making involves the optimization of multiple costs (Drugowitsch, et. al., 2012). Decision-making tasks may involve cognitive costs (i.e. sensory processing, memory, attention) and the costs of physical effort in addition of time, all eventually involved in the process of accumulating evidence. These costs in fact unfold in time and have a temporal structure that varies from context to context. Thus, to efficiently keep track of the costs that build up in time, one needs to factor in the physical costs as well. Under this conceptualization, physical costs can also contribute to urgency consistent with that of time pressure. Luckily, there is increasing research tackling the effects of physical costs in relation to decision-making. For instance, there is currently enough evidence to support that the physical cost of actions influences the dynamics of decision-making. Burk and colleagues (2014) showed that increasing the physical cost needed to execute response movement leads to less changes of mind during a decision-making process. Similarly, Marcos and colleagues (2015) tested whether motor cost of response actions influence the performance in a binary decision-making task. They found that when the two response actions have different levels of motor cost, there is a bias of subjects to choose the less effortful option. This implies that the motor costs involved in the response impact the choice. Morel and colleagues (Morel, et. al., 2017) have found that the effects of different levels of effort was not proportional to the metabolic cost of the movements, but rather to perceived levels of effort. This has resulted in the interpretation that physical effort has a way of influencing the decisions not merely as a function of their metabolic costs, but instead as a function of the perceived effort (Cos, 2017).

According to the findings reviewed above, it seems plausible to associate effort-related effects in decision-making to the signal of urgency, whose main function has been claimed to be taking costs into account. Although these findings suggest that a common urgency signal may control the speed and timing of the response movements (shared invigoration hypothesis; Cisek & Thura, 2018, Thura, 2020), few studies have addressed the effects of physical effort during evidence accumulation The contingency of evidence accumulation on effort gets us closer to real life scenarios in which motor actions are necessary to collect and sustain sensory evidence (Ayhan & Ozbagci, 2020). The studies that have come closest to address this scenario are dual task studies which measure performance in a cognitive task concurrent with a secondary, effortful task. For instance, Park and colleagues (2021) studied how visual attention is influenced by an ongoing simultaneous physical effort expenditure. They found that moderate levels of physical effort shorten reaction times in a visual search task, but also increase distractor interference effect due to less efficient attentional mechanisms. Considering that attention has a crucial role in decision-making, it can be claimed that effortful action can influence decision-making as well in situations that require slow accumulation of evidence. Yet, this hypothesis has not been tested. Therefore, to understand how physical effort costs influence the decision process and whether they have similar effects with time-related costs, we need experimental paradigms that incorporate effortful actions within the period of decision, but also contingent to evidence accumulation. Such an effort-contingent evidence accumulation task is representative of many real-life situations, and it has therefore important value in terms of ecological validity.

The goal of this study is to address the influence of contingent physical effort on performance in a visual decision-making task, and test whether urgency is sensitive to physical effort. This question requires a task that incorporates an effortful physical action to initiate and uphold the evidence gathering that is needed to make a decision. Thus, we have used a manual hand press action during a perceptual discrimination task, with manipulations of both the time pressure (by imposing response deadlines) and exerted physical effort necessary to accumulate evidence. Our main hypothesis was that if contingent physical effort and time pressure contribute toward an urgency signal, then they should impact SAT dynamics in the perceptual decision-making task, in convergent ways. That is, increasing effort should resemble stricter deadlines, so that end up in shorter reaction times and lower accuracies.

2. Methods

2.1. Participants

Twelve participants (8 females, mean age = 24.3 years., [19-33]) have completed the experiment. Participants were invited through the database of the Center for Brain & Cognition (Universitat Pompeu Fabra) and were given 20 euros in exchange of their participation for 2 hours. All participants were right-handed, had normal or corrected-to-normal vision and had no history of motor problems related to use of their left hand, arm and wrist. They all signed an informed consent form and a data privacy form. The experiment was approved by an institutional ethical committee

(CIREP, Universitat Pompeu Fabra) and all methods were performed in accordance with the relevant guidelines and regulations. Since this was a novel study, we could not optimize the sample size with an analytic approach before the data collection. Because of time constraints, we had planned to recruit 20 participants. After hitting that number, we had to exclude data from 8 participants due to low performance (< 50% correct responses in all stimulus strengths). Considering that many psychophysics studies recruit lab members or people who are familiar with perceptual experiments into their studies, this high incidence of inadequate performance in our data set is due to the recruitment protocol we have used. The participant pool was naïve to long and effortful psychophysical paradigm; so that we presume that some were not motivated to perform better. Thus, we continued our analysis with the data from 12 participants. It is also relevant to note that we used 125 trials per effort/deadline condition, which is a sufficient number compared to other random dot motion studies. Similarly, when compared with many other motor-learning experiments which commonly has between 8 to 12 participants (Moskowitz, et. al., 2022), our sample size is adequate to test our hypothesis.

2.2. Apparatus

The experiment was conducted in a darkened room. Participants sat in front of a CRT monitor (Sony Multiscan G520; refresh rate 60 Hz; 1024 × 768 pixels) which was placed 60 cm away from the participant’s head (as it rested on a chinrest). Seat and chin-rest height were adjusted at a comfortable position for each subject. To measure effort, a hand dynamometer (Vernier HD BTA, with Arduino USB adaptor) was used. Stimuli and experimental scripts were programmed in Matlab, PsychToolBox.

2.3. Visual Stimuli

The task consisted of motion discrimination 2AFC of Random Dot Kinematograms, RDK (Figure 1; Britten, et.al., 1992, Shadlen & Newsome, 2001). The RDK consisted of a cloud of white dots (2-pixel radius) moving at 5 deg/sec within a circular area of the screen, aperture size of 5 degrees of visual angle, and density of 16-7 dots/deg^2. The detailed stimulus features and algorithm is described in Gold and Shadlen’s (2003) work. Coherence was manipulated as the proportion of dots moving coherently either towards left or right, amongst otherwise randomly moving dots within the aperture. The set of dots moving coherently was randomly selected at every time step, except that all dots had a maximum life time of 4 frames moving in the same direction. This feature of short lifetime is implemented to make sure that it is not possible to track only one coherent dot and figure out the answer. Some dots can move out of the window if the starting position of the dot is close to the edges before 4 frame life time, after which it re-emerged at another random location. So, the participant needs to observe the general motion rather than individual dots. There were five levels of coherence which are logarithmically scaled as it is the standard in the field: .032, .064, .128, .256, .512.

2.4. Experimental Task and Effort Manipulation

Participants performed a 2AFC direction discrimination task on the RDKs described above. To study the effects of motor effort on the ongoing decision process, we included three effort levels: No Effort, Low Effort, and High Effort. The No Effort condition served as a baseline situation in terms of requiring no motor action for stimulus viewing, so that equating it to the common way RDK experiments have been carried out in the literature. In the two effort conditions, instead, the participants were required to press and hold a dynamometer with the left hand to initiate and maintain the stimulus on the display (Figure 1, middle). Each initiation phase started with the presentation of white fixation cross at the center of the screen, which prompted participants to press and reach the required force level for a trial to begin (there was a maximum wait time of 2s). Once the force threshold was reached, the RDK stimulus appeared on screen and, in order to keep the stimulus on-screen, the participant had to sustain the effort exertion above the required threshold until a response. The response, with the right dominant had, was made via a keyboard press (left and right arrow keys, to indicate whether the overall motion is towards left or right respectively). We also manipulated response deadline by limiting the maximum viewing time and responding, which was either 4s or 1.5s. If the grip force fell under the threshold before a response was given or if a participant had not responded by the deadline (4s or 1.5s), that trial aborted, and the fixation cross turned yellow to notify the participant that the trial was invalid. The same trial was repeated at a random later trial in the session, securing the total number of trials. When a choice was made, the fixation cross turned red for incorrect responses and green for correct responses (Figure 1, bottom). The feedback period with the color-coded fixation signal took 1.5 seconds. Then, the fixation cross turned white again, which indicated the beginning of the initiation phase of the next trials.

In the No Effort condition, the stimuli appeared without a hand press and the participant had to passively watch stimuli and make a decision. To make the temporal structure similar across the conditions of the experiment, there was a delay before the stimulus appeared akin to the initiation phase in effort trials. For this delay, we used the individual's average initiation duration from the effort trials as a pre-stimulus delay plus a small uniformly distributed random jitter between -.1 and .1 s. Thus, each subject had to start the experiment with one of the effort conditions, to be able to calculate average pre-stimulus delay.

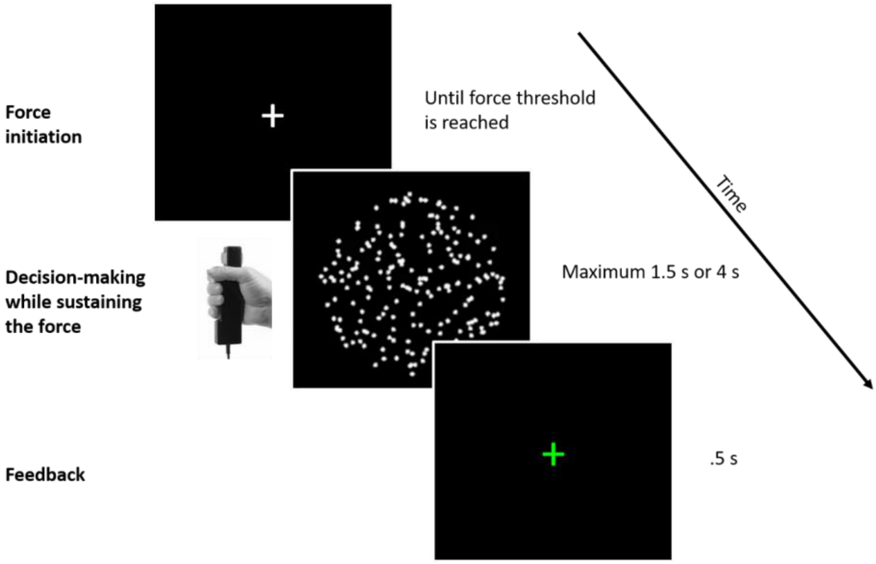

Figure 1. Trial Sequence. Each trial starts with a blank screen with a white fixation cross. Participants initiate pressing the dynamometer and until the force threshold is reached while the white fixation remains on the screen. After the threshold is reached, the RDK stimulus appears and the participant has to make a decision about the motion direction within 1.5s or 4s. After a response is made, fixation cross changes the color to red (incorrect) or green (correct).

2.5. Procedure

Effort calibration

Before starting the decision-making task, each participants' potential force exertion was calibrated. In this phase, participants were asked to press the dynamometer momentarily as hard as possible, three times. The average of the maximum values from the three presses were taken as Maximum Voluntary Control (MVC) for that participant. Then, we took 10% and 25% of the individual MVC as the effort thresholds for the Low and High Effort conditions.

Experiment

After calculating the MVC, each participant proceeded with a training phase which consisted of 15 trials, consisting of the repetition of 3 mid-level coherences, with a deadline of 4s. The purpose of the training was to familiarize the subject with the hand grip and perceptual task at the same time. Training was repeated until participants reached at least 70% accuracy in the 2AFC motion discrimination task. When a participant successfully finished the training, they proceed to the experimental blocks. In the experiment, there were two fully crossed between-block manipulations: physical effort (No, Low and High Effort) and duration deadline of trials (1.5 s and 4 s). The order of the blocks was chosen randomly, except that the No Effort blocks were never the first, to be able to calculate the average trial initiation period for No Effort condition from the participant's effort condition trials. Subjects had freedom to take short (5 minute) breaks in between the blocks. Within each block, 25 repetitions of each 5 coherence levels were presented in random order, which makes a total of 125 trials per block, and a total of 750 trials overall (plus, eventual repetitions of invalid trials, on average 3% per subject).

3. Results

3.1. Reality check: Force Exertion in Low and High Effort

In both effort conditions of this experiment (Low and High), participants were required to apply a minimum level of force on the dynamometer to initiate the onset of the visual stimulus and proceed with the trial. However, since we did not control for the precise level of force exerted, it may have been possible that the participants could have pressed stronger than required, equalizing the Low and High Effort conditions in terms of exertion. To rule out this possibility, we gauged the overall exertion throughout the trial to ascertain that Low and High Effort conditions were indeed different. Figure 2 shows that this was the case regardless of trial timeout (1.5 or 4s). We did paired-samples t-tests to test whether average forces applied Low Effort condition was lower than in High Effort condition. The result showed that in both 4s and 1.5s deadline conditions the average force applied in each condition was significantly different (t(11) = -7.2, p < .001, Cohen's d = -2.1 and (t(11) = -3.4, p = .003, Cohen's d = -.99) throughout the average duration of the trial.

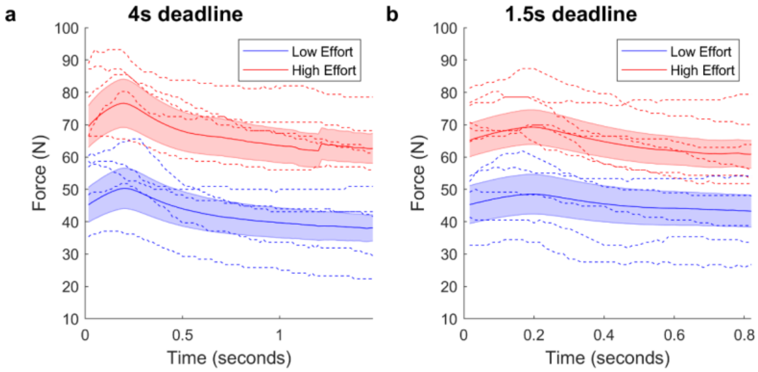

Figure 2. Average force (in Newtons) exerted during the 4s (**a**) and 1.5s (**b**) deadline conditions. The solid lines and shades correspond to overall mean and standard error of the mean. Dashed lines are some individual trial data from one representative participant. Note the different x-axis ranges, which correspond to the average reaction times in Low & High conditions in the corresponding deadline conditions.

3.2. Speed versus Accuracy

To test the main hypothesis, we first focused on reaction times and accuracy. If effort drove urgency as hypothesized, we ought to see reaction time (RT) shortening as a function of effort at the expense of accuracy, especially in the long deadline condition where there is more room for speeding up. As Figure 3a-b illustrates, physical effort shortened RTs in both the 4s condition (No Effort = 1.82s, Low Effort = 1.57s, High Effort = 1.39s, p = 0.002, $\eta^2 = .7$) and 1.5s condition (No Effort = 0.91s, Low Effort = 0.89s, High Effort = 0.77s, p < 0.001, $\eta^2 = .4$). To further test the combined effects of effort intensity and deadline on RTs, we conducted a two-way repeated measures ANOVA on RTs with deadline and effort intensity as independent variables (a Shapiro-Wilk test of normality showed that the normality assumption was not violated, $p > .05$). The results showed that both deadline and effort intensity exerted a significant influence on RTs ($F(1,11) = 69.5$, $p < .001$, $\eta^2 = .69$ and $F(2,22) = 12.1$, $p < .001$, $\eta^2 = .07$, respectively). The interaction between deadline and effort also came out significant ($F(2,22) = 4.4$, $p = .025$, $\eta^2 = .02$), as the speeding up effect of effort was smaller under the more strict deadline. We also conducted regression analysis per participant to get a more detailed picture of how Coherence, Deadline and Effort all influence RT. The results of these analyses can be found in Supplementary Analysis 1. Overall, effort speeded up the decisions, in a way similar to a manipulation of the deadline. This befits the notion that both time pressure and effort contribute to a common urgency signal.

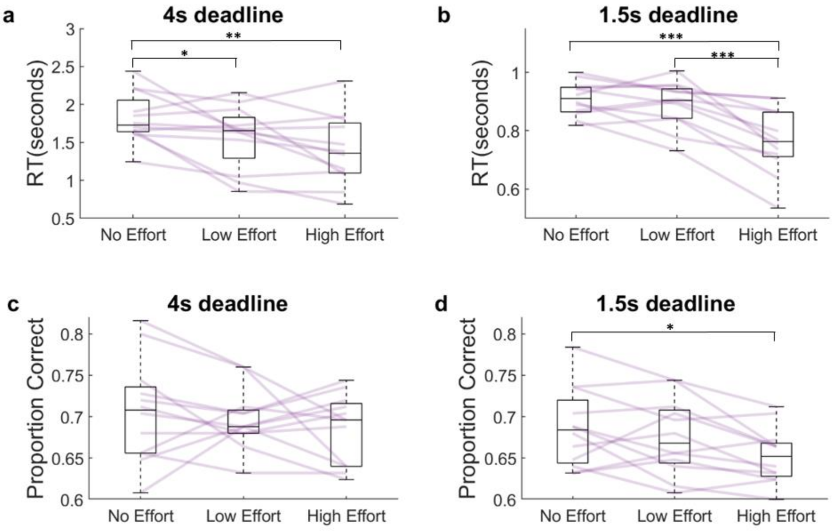

Figure 3. Average reaction time (**a, b**) and accuracy (**c, d**) box plots. Purple lines represent individual data. Asterisks indicate significance of difference (* is p <.05, ** is p < .01, *** is p < .001) **a-b** Reaction times from 4 and 1.5s deadline conditions, respectively **c**-d Proportion of correct responses from 4s and 1.5s deadline conditions, respectively.

Next, we assessed the average accuracy for each deadline and effort condition, collapsing across coherence levels (Figure 3c-d). Physical effort did not have a significant effect on the proportion of correct responses in the 4s deadline (Figure 3c, no effort = .71, low effort = .7, high effort = .69, p = 0.54, η^2 = .05), but it significantly reduced correct responses in the 1.5s deadline blocks (Figure 3d, No Effort = .69, Low Effort = .68, High Effort = .65, p = 0.013, η^2 = .33). We again conducted a two-way repeated measures ANOVA on the proportion correct responses with deadline and effort as independent variables. We again ensured that normality assumption was not violated (Shapiro-Wilk tests, p > .05). The results showed that the effect of deadline on accuracy was significant (F(1,11) = 8.07, p = .016, η^2 = .12). The effect of effort on the other hand showed a trend in the expected direction, but it did not reach significance (F(2,22) = 3.4, p = .051, η^2 = .09). The interaction between the two variables was not significant (F(2,22) = .25, p = .78, η^2 = .007). In general, effort did not reduce response accuracy as strongly as the manipulation of the deadline, although, as previously described, they both significantly influenced the RTs. We conducted per-participant regression analysis to assess how coherence, deadline and effort influence choice accuracy. These are summarized in Supplementary Analysis 2. Altogether, the proportion correct results are consistent with the general hypothesis that effort tends to exert a qualitatively similar influence than response deadline on performance, albeit slightly weaker under the specific parameters of this study.

3.3. Psychophysical analysis

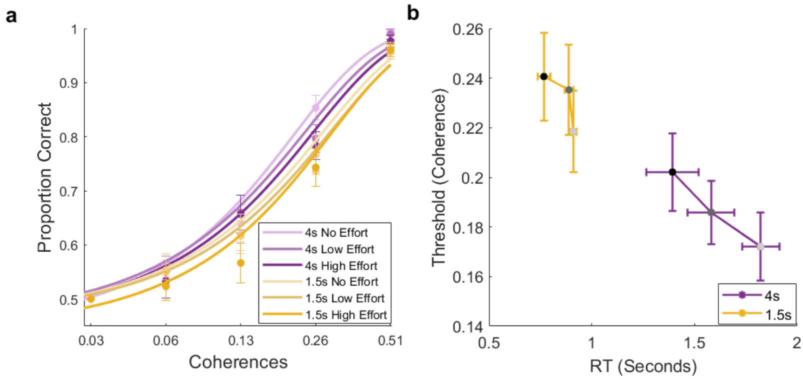

Figure 4. a. Average Psychometric Curves. Proportion of correct responses as a function of stimulus coherence. Here, average performance from all participants plotted for illustrative purposes. Shades of purple belong to 4s deadline conditions and shades of yellow correspond to 1.5s deadline conditions. Increasing color tone indicate the effort level. **b**. Average of psychophysical threshold (y-axis) and RT (x-axis) for each condition. Purple represents the 4s deadline conditions. Yellow represents the 1.5s deadline conditions. The shade of the points indicates the effort level, light grey: No Effort, medium grey: Low Effort, black: High Effort.

We used a GLM with a logit link function to fit individual proportion correct data as a function of coherence, for each condition. We estimated individual discrimination threshold as the coherence value corresponding to 75% correct performance and analyzed this threshold as a function of deadline and effort in a two-way repeated measures ANOVA (Shapiro-Wilk tests, $p > .05$). Both deadline and effort had a significant influence on discrimination threshold (F(1,11) = 12.2, p = .005, η^2 = .21 and F(2,22) = 4.3, p = .026, η^2 = .07, respectively), and their interaction was not significant (see Table 1 for the average threshold values in each condition). Figure 4a shows that both shorter deadlines and stronger efforts led to higher thresholds, that is, worsened discrimination performance. To better convey RT and performance effects combined we have illustrated mean RTs and discrimination thresholds per condition, in Figure 4b. Overall, our results show that effort speeds up RTs and increases the threshold under both deadline conditions. It also became evident that with a more relaxed response deadline, the effect of effort is even more visible, in keeping with the main analyses. Considering that effort builds up with time, its influence should be stronger at longer timescales, whereas under a stricter deadline the relative speed up / threshold increase effects due to effort are weaker because there is already pressure for fast responses. This is the kind of additive effect one may expect if the two factors (time and effort) converge on the same process. Our hypothesis is that this convergent process is in fact urgency.

Deadline	**Effort**	**RT (s)**	**Prop. Correct**	**Threshold (Coherence)**	**Slope (Coherence)**
Long	No	1.82 (.09)	.71 (.017)	.17 (.017)	9.5 (.66)
	Low	1.57 (.11)	.70 (.011)	.19 (.011)	7.9 (.6)
	High	1.39 (.13)	.69 (.011)	.21 (.014)	7.1 (.54)
Short	No	0.91 (.017)	.69 (.014)	.22 (.017)	7.0 (.8)
	Low	0.89 (.023)	.68 (.014)	.23 (.02)	6.3 (.54)

	High	0.77 (.03)	.65 (.014)	.24 (.017)	6.7 (.69)

Table 1. Mean Reaction Time, Accuracy, Threshold and Slope of psychometric curves for each condition. Standard error of the mean (SEM) is written in parenthesis.

Another crucial insight to gain from the psychophysical analysis is the slope of the curves. The slope indicates the amount of change in stimulus intensity causing a change in the performance, therefore providing us with an idea about sensitivity. To analyze the sensitivity, we conducted a repeated measures ANOVA with deadline and effort as independent variables and slope as a dependent variable (Average values can be seen in Table 1). The results showed that deadline had a significant negative effect on the slope of psychometric curves (F(1,11) = 16.2, p = .002, $\eta^2 = .17$), and effort had a significant positive effect (F(2,22) = 5.4, p = .01, $\eta^2 = .1$). Thus, these results indicate that shorter deadlines and stronger effort led to less precise discrimination of motion direction.

3.4. Force Fluctuations Trial by Trial

After assessing the influence of effort on RT and choice by comparing the conditions of No, Low & High Effort, our remaining question was whether the trial-by-trial fluctuations in effort (i.e. the exerted force over the dynamometer) could predict RT and choice accuracy. To this end, we focused on the Low and High Effort conditions separately, by fitting linear regression models to predict log(RT) from Coherence and Average Force per trial, per participant and condition (4s Low Effort, 4s High Effort, 1.5s Low Effort and 1.5s High Effort). The results showed that Coherence was a significant predictor of log(RT) in all 12 participants and in all deadline/effort conditions (range of the coefficient = [-2.5, -.08], $p < .05$). However, the trial force was a significant predictor only in a small subset of participants for each condition (range of the coefficient = [-.008, .001], $p < .05$ 4s - Low Effort: 7 participants, 4s – High Effort: 3 participants, 1.5s - Low Effort: 3 participants, 1.5s -High Effort: 2 participants). In short, fluctuations of the force on a trial-by-trial basis were a poor a predictor of the reaction time in the majority of participants. Importantly, it became evident that the strongest effect of force on RT was in the condition in which the force could vary the most (namely, 4s - low effort condition). Stricter deadline conditions and higher effort requirement may have lowered the variability in force/RT, thus making it more difficult to see trial by trial fluctuations. In fact, the standard deviation of both force and RT is the largest in 4s low effort compared to higher effort or shorter deadline conditions (Figure 5).

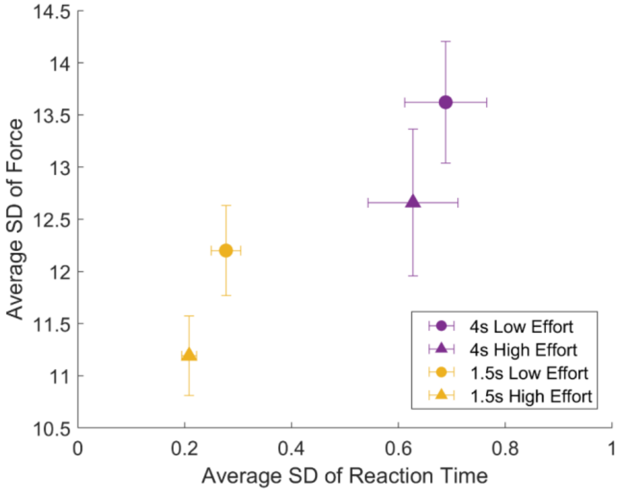

Figure 5. Average standard deviation of RT (x-axis) and Force (y-axis) for each effort/deadline condition. Purple represents 4s deadline conditions, yellow represents 1.5s deadline conditions. Circle indicates Low Effort and triangle indicates High Effort conditions.

We also conducted a Logistic Regression analysis to predict choice (correct or incorrect) from Coherence and Average Force in a trial, per participant and per condition. Coherence was a significant predictor of choice for all subjects ($p < .05$). However, force was not significant in any participants for any condition. Therefore, the trial by trial fluctuations in applied effort on the dynamometer were not sufficient to explain trial to trial choice accuracy, at least under the conditions of this experiment.

3.5. Lack of Left/Right Bias

So far we have estimated discrimination threshold and correct response measures lumped over direction of motion of the stimulus to gain more stable measures, as this variable is orthogonal to our hypothesis. However, because the task involved choices based on the left or right direction of stimulus motion, we decided to check if there was any significant directional bias across participants. To this end, we fitted psychophysical curves for probability of right choice as a function of each level of coherence, distinguishing between leftward motion (negative sign by convention) and rightward motion (positive sign). A repeated measures ANOVA with effort and deadline as independent variables and bias as a dependent variable showed that neither deadline nor effort exerted a significant effect on bias (F(1,11) = 1.05, p = .33 and F(2,22) = 1.07, p = .36, respectively and Shapiro-Wilk tests, p > .05). For completeness, we also ran an ANOVA on the slope, and found that deadline did not exert a significant effect on slope whereas effort had a significant effect (F(1,11) = 3.1, p = .1 and F(2,22) = 12.6, p < .001, respectively and Shapiro-Wilk tests for normality, p > .05). Group means of bias and slope are shown in Table 2.

Deadline	**Effort**	**Bias (Coherence)**	**Slope (Coherence**
Long	No	-.01 (.017)	7.8 (.6)
	Low	.01 (.01)	6.4 (.49)
	High	.01 (.021)	5.6 (.35)
Short	No	.02 (.017)	6.3 (.52)
	Low	.01 (.005)	6.1 (.43)
	High	.02 (.017)	5.4 (.37)

Table 2. Mean Bias and Slope obtained from fitting psychometric curves for left and right choices. Standard error of the mean (SEM) is written in parenthesis.

4. Discussion

Physical effort is an important aspect in many everyday life decisions, as energetically costly actions (for example hand, head or whole-body movements) are often required to gather critical information to make decisions. This study tested the hypothesis that when physical effort is required to accumulate task-relevant sensory evidence, it influences urgency and, consequently, the speed accuracy trade-off in decision-making. We used an experimental task in which an effortful action was required to accumulate sensory evidence to carry out decisions, and studied if effort intensity induced an urgency effect of similar consequences to that of imposing time constraints. Our results showed that increased effort speeded up the RTs and diminished performance, and that the influence of effort interacts with that of time pressure, as it diminishes under a strict deadline. This reinforces the notion that effort influences urgency, therefore combining with other urgency-related factors, such as time pressure.

In general, our work is in line with others before that have shown motor effort can alter decision-making (Burk, et. al., 2014, Cos, 2017, Marcos, et. al., 2015, Shadmehr et. al., 2016). However, these previous studies have focused on the effort required to execute the response movement, but not the effort required to control and sustain evidence accumulation, which was the focus of this study. The novel result here is that physical effort required to accumulate information brings about speed-accuracy adjustments. In addition to shortening of reaction times due to effort, we also reported that effort had a detrimental effect on accuracy, albeit weaker. However, motion discrimination thresholds from psychophysical curves demonstrated that increasing effort significantly worsened the discrimination performance too. Hence, we can conclude that effort impairs performance in addition to shortening the reaction times. Overall, these results indicate that physical effort modulates the cost structure of a decision-making process, akin to temporal constrains. This supports the initial hypothesis that effort costs contribute to a common urgency signal, together with time pressure.

Urgency or collapsing bound models have repeatedly shown that optimal decision-making has to take elapsed time and temporal restrictions into account (Drugowitch, et.al., 2012, Cisek, et. al., 2009). This brought many scholars to think of urgency as a signal to modulate overall reward rate by factoring in the cost of decision time (Carland, et. al., 2019). Here, we took this understanding one step further by addressing whether the urgency signal takes the effort-related costs incurred during the decision-making process into account as well. Based on physiological findings, this is a plausible hypothesis. The basal ganglia, a brain area initially thought to modulate rewards (Houk, et. al., 1995, Schultz & Romo, 1992) has been proposed to mediate urgency related signals (van Maanen, 2016). When it comes to physical effort and basal ganglia activation, Kurniawan and colleagues (2011) have shown that physical effort discounts the action value and basal ganglia has a role in effort representation and value. It is plausible then to think that the basal ganglia could process the physical costs that discounts rewards. Thus, there is ample support for the claim that the same mechanism related to basal ganglia and dopaminergic activation can be responsible for processing both effort and time related costs (van Maanen, 2016, Thura & Cisek, 2017).

The effect of effort on the urgency of decisions might be mediated via some representation of time, since urgency requires a representation of time passage. Such mediation would imply that there is a relation between action and time estimation. Indeed, there is plenty of support in the literature about the effects of a concurrent motor action on time perception. For instance, Wiener and colleagues (Wiener, et. al., 2019) showed that the precision of time estimates was higher when subjects carried out a manual reach action, compared to when they remained still. They concluded that motor engagement brought a perceptual advantage. Other studies have shown that perceived time gets compressed around the moment of a movement (Tomassini & Morrone, 2016, Hagura, et. al., 2012, Press, et. al., 2014, Ayhan & Ozbagci, 2020). Although there is no general consensus on how movements influence time perception (increasing precision, or compressing subjective time), it is safe to argue that an ongoing motor action can alter time perception. Thus, a question worth testing in future research is whether one mediating factor behind shorter reaction times under higher physical effort can be the altered time perception due to the ongoing motor action; note that, according to our results, it would not be (only) acting per se, but the amount of effort put in the action, what matters.

Apart from time perception, ongoing motor action and effort have also been argued to influence visual attention. Park and colleagues (2021) have shown that under effortful actions, visual search seems to proceed faster. They concluded that moderately effortful motor actions could enable faster cognitive processing. In order to understand the interactions between effort and speed of cognitive functions, further studies should address the effect of effort on diverse tasks and diverse temporal contexts. Similarly, more detailed analysis of whether this faster cognitive processing imposes significant drops in precision and task performance are needed. According to our own results, admittedly limited in this respect, we could speculate that if effort speeds up cognitive processing, it does so at the expense of accuracy, albeit very weakly so.

The present study addressed the effects of effort on perceptual decision-making, but we need to consider that physical actions induce increases in arousal, and arousal variations can mediate effort-related updates in decision-making. Arousal is commonly gauged by pupil size, as the noradrenergic system is directly linked to expansion and constriction of the pupil. By measuring pupil size in a decision-making task, Naber and Murphy (2020) have found that larger baseline pupil size predicts faster reaction times and Steineman and colleagues (2018) have reported that under strict time pressure baseline pupil size is higher than liberal conditions. There is also evidence that physical effort influences arousal. For example, Zenon, and colleagues (2014) have measured the subjects' pupil sizes during force production via a hand dynamometer and found that larger force brings larger phasic arousal. Hence, to clarify whether ongoing physical effort has an effect on decision process via the arousal system, we suggest to check pupil size in similar task design like ours in future studies. In this way, the differences between deadline and effort manipulations could be compared in terms of their impact on arousal levels and test whether heightened arousal correlate with SAT dynamics in a decision-making task.

In conclusion, in this study we addressed whether physical effort intensity induces an urgency effect converging with those induced by time pressure. We believe our results are supportive of this hypothesis. In addition, our findings extend our understanding of decision-making in a more ecological context given the many cases in everyday life where physical effort is needed to sample information, from simply moving the eyes or the head to body parts actions and whole body movement. By combining an effortful motor action contingent with a classic perceptual decision-making task, we have shown that increased physical effort sped up reaction times and weakly lowered performance in terms of accuracy, and perceptual discrimination threshold, as well as in terms of precision. These effects are similar to, and combine with those of strict deadlines in the sense that they both imposed increased cost and thus ended up with speed-accuracy alterations. We argue that urgency is a mechanism which factors in time-related and effort-related costs into account during a decision-making process, which eventually impacts speed-accuracy adjustments through a common currency.

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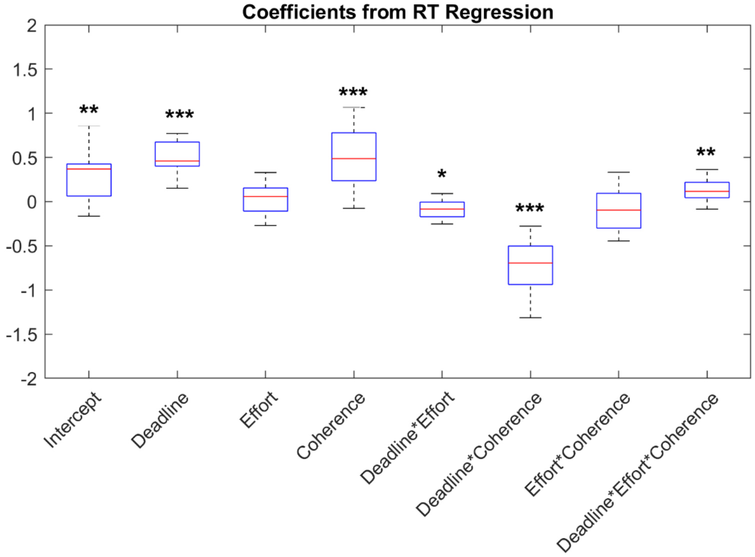
Supplementary Analysis

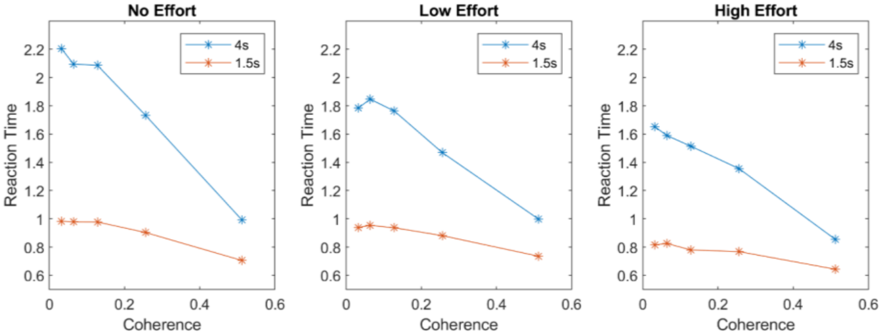
1. Regression over reaction times

To assess in depth how coherence factors in RT and interacts with Deadline and Effort, we fitted Linear Regressions per participant to predict RT from Deadline, Effort and Coherence and their interactions. After fitting these regressions for each participant, we have taken the coefficients and conducted t-tests for each of them to see if they are significantly different from 0. The results have shown that except Effort and Effort*Coherence interaction, all regression terms were significantly different from 0.

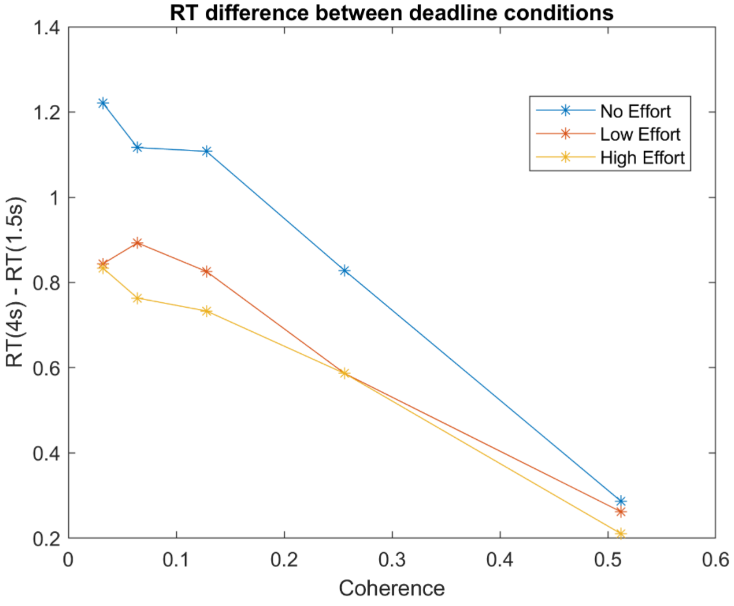


Supplementary Figure 1. Boxplots of coefficients from Linear Regressions predicting Reaction Time. Asterisks indicate significance (* = p < .05, ** = p < .01, *** = p < .001).

In order to interpret the significant interaction effects better, we plotted the average RTs for each coherence and each condition. In Figure S2, we can see the Deadline*Coherence interaction from checking the slopes of blue and orange lines. Similarly, Deadline*Effort interaction is the overall separation of blue and red lines across the three boxes. To demonstrate the three-way interaction of Deadline*Effort*Coherence more clearly, we presented Figure S3, in which we can see that RT differences between two deadline conditions is modulated by coherence and larger in No Effort condition compared to Low and High Effort conditions.



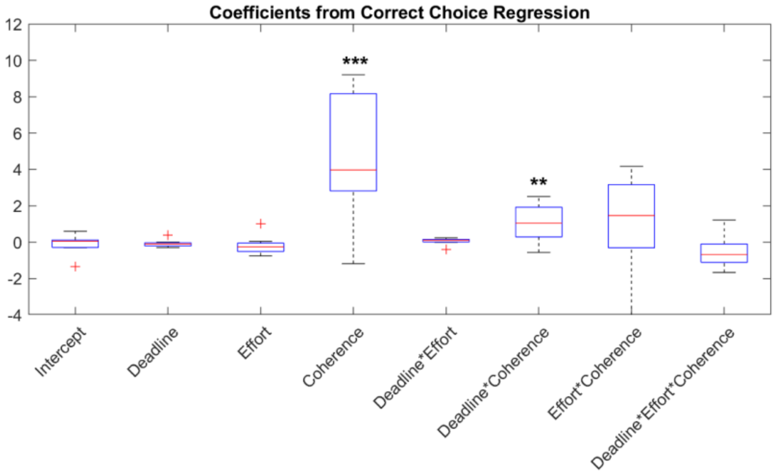
Supplementary Figure 2. Average RT (y-axis) for each Coherence (x-axis). 4s and 1.5s deadline conditions are represented in blue and orange lines respectively.



Supplementary Figure 3. The difference between average RTs in 4s and 1.5s deadline condition. x-axis indicates the Coherences and each line belongs to a different effort condition.

2. Regression over reaction times

To assess in depth how coherence factors in correct choice and interacts with Deadline and Effort, we fitted Logistic Regressions per participant to predict Correct Choice from Deadline, Effort and Coherence and their interactions. After fitting these regressions for each participant, we have taken the coefficients and conducted t-tests for each of them to see if they are significantly different from 0. The results have shown that only Coherence ($p < .001$) and Coherence*Deadline ($p < .01$) interaction terms had coefficients significantly different from 0.



Supplementary Figure 4. Boxplots of coefficients from Logistic Regressions predicting Correct Choice. Asterisks indicate significance (* = p < .05, ** = p < .01, *** = p < .001).

2.3. Physical effort induces changes into pupil-linked arousal as well as modulating speed and accuracy trade-off in decision-making

Ozbagci, D., Cos, I., Soto-Faraco, S., Moreno-Bote, R.

Physical effort induces changes into pupil-linked arousal as well as modulating speed and accuracy trade-off in decision-making

In preparation

Physical effort induces changes into pupil-linked arousal as well as modulating speed and accuracy trade-off in decision-making

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ABSTRACT

Effort of motor actions incur an optimality problem for decision making. Similar to time costs, a decision maker has to evaluate how much physical effort needs to be devoted in order to complete a decision. In our earlier work, we established that physical effort induces faster responses and lower performance in a perceptual decision making task. This effort-induced urgency could potentially be related to elevated arousal levels under effortful actions. In order to test this, we carried out a random dot motion experiment in which the stimulus was contingent on a hand press action with different intensities of effort. We hypothesized that physical effort modulates pupil-linked arousal. Furthermore, we predicted that the changes in arousal would correlate with the speed and accuracy of responses. The results showed that physical effort increased the tonic pupil sizes and tonic pupil sizes were significantly correlating with speed and accuracy of responses under each effort regimen. Hence, we concluded that effort-related changes in speed and accuracy trade-off are likely to be modulated by arousal.

1. Introduction

To make decisions, one must expend cognitive and physical costs that comes from the effort of response execution or information sampling. According to an economic framework, this can be understood with the notion of utility maximization; all costs are compared against the potential rewards to optimize the decision process (Drugowitch et al, 2012, Kennerley. Et. al., 2009). Although delay and time-related costs have been well-studied and formalized within that framework (Kacelnik et. al., 1997, Wittmann, et. al., 2007) our understanding of how physical effort factors in in the decision making process is still limited (Kurniawan, et. al., 2011). Thus, further understanding is needed regarding the mechanisms behind the effort-based modulations of decision making. In our previous work we have reported evidence that physical effort induces urgency in a similar way to time constrains (Ozbagci et al., 2022). In the present study we aim at investigating whether this effort-based changes in urgency and SAT can be related to arousal.

Before delving into physical effort in decision making, it makes sense to discuss how motor costs influence decisions. Generally, organisms tend to choose the less energy costly response option in decision making (Cos, et. al., 2011), and make less changes of mind if the change requires high physical cost (Burk, et. al, 2014). These findings mean that the brain takes motor costs into account whilst executing decisions and therefore physical effort modulates the decision making process (Cos, 2017). Morel, et. al (2017) took it further and demonstrated that physical effort does not only depend on the metabolic cost of action but also the duration of the effort, thus their work supported the notion that both motor control and decision making share similar optimization mechanisms. A similar link between motor control and decision making is suggested by the ‘shared regulation hypothesis’ by Cisek & Thura (2018). This hypothesis states that decision urgency (defined as a cost signal that tracks the ongoing time and ensures to respond with less certainty as time goes by so that the opportunity to gain reward is not missed) not only influences decision formation, but also motor execution (invigoration) (Thura, 2020).

As urgency has been suggested to have a relation with regulation of motor responses, in our previous work we hypothesized that urgency could also track physical costs (i.e. effort) on top of time-related costs (Ozbagci, et. al., 2022). The novelty of that study was that effort was made contingent on the information sampling, but not on response. That is, effort was required to sample information which was relevant for the decision but orthogonal to the actual response. This is an ecologically relevant case since sampling information to reach a decision can often require physical effort. As a result of that experimental work, we reported that increased physical effort lowered the RT as well as proportion of correct responses. We concluded that effort contributed to urgency, in a similar way as time pressure. However, there was still a lack of understanding about the mechanisms which could underlie these effort-based alterations in speed, accuracy and perceptual decision-making performance. One potential mechanism that we consider as a contributing factor to mediate effort-related SAT adjustments via urgency is arousal. Arousal is considered a global brain state that is related to the level of activation and integration across brain areas, and it is modulated by emotion, movement, and sleep (Humphreys & Revelle, 1984, Whissel, et. al., 1986). Since motor actions induce certain level of arousal, it is important to address whether the effects of physical effort on decisions that we and others report are partially due to changes in arousal.

Arousal modulates various behavioral and cognitive phenomena. For instance, according to classical Yerkes-Dodson Curve (Yerkes & Dodson, 1908), moderate levels of arousal bring about most optimal behavioral performance whereas very low and high levels induce impairments. If arousal is too low, it indicates disengagement with a task and too high indicates an agitated state which also is a marker of attention difficulties. Locus Ceuruleus (LC) in the brain stem is the area that controls arousal by releasing of neurotransmitter norepinephrine (NE), and its connections with various cortical and subcortical structures explain the widespread impact of arousal throughout the brain (Sara & Bouret, 2012). Because LC regulates pupil size, it is common to use pupil size as a measure of arousal (Krugman, 1964, Granholm & Steinhauer, 2004). Although pupil’s main response is to light, both phasic and tonic changes in pupil size under equal luminance have been associated to changes in cognitive performance (Eldar, et. al., 2013). For instance, larger tonic pupil size (baseline changes) has been related to faster reaction times (Shriver, et. al., 2018) and poorer performance due to increased distractibility (Zenon, 2019) and response variability (Van Kempen, et. al., 2019). Phasic pupil changes on the other hand are inversely correlated with the tonic levels of arousal (Aston-Jones & Cohen, 2005) and have usually been regarded as indicators of better performance (Colizoli, et. al., 2017, van Kempen, et. al., 2019).

Speed and accuracy of responses are also subject to changes as a result of pupil-linked arousal. For instance, Naber & Murphy (2020) have found that pupils dilated more under speed pressure and larger baseline pupil size predicted faster and less accurate response movements. Hence, the researchers concluded that arousal has a critical role in gain modulation of neural processing which can explain speed-accuracy adjustments. Murphy, et. al. (2016) as well proposed that global gain modulation in the brain which can be tracked by pupil-linked arousal is subject to changes due to urgency of response. They reported larger pupil responses as a result of short deadline imposition and asserted that pupil-linked arousal and urgency are related processes. Thus, there is ample support for the claim that arousal can be a key mechanism behind the reward optimization in the face of costs. On the grounds that physical effort is a source of cost over various cognitive processes, we claim that pupil-linked arousal undergo changes as a function of physical effort. Zenon, et. al., (2014) have conducted a study in which they recorded pupil signals during effortful manual contraction and founded that larger physical effort predicted larger pupil responses. In a similar vein, Varazzani, et. al. (2015) presented MRI and single cell recordings in monkeys during effort-based decision making task. They reported larger NE release in LC with increased physical effort. Since, LC controls pupil size, that work implies that physical effort induces arousal changes. Physical effort may influence decision process via increasing the overall arousal state.

Hence, from the research discussed above we learn that (1) pupil-linked arousal tracks speed-accuracy adjustments and (2) pupil-linked arousal tracks physical effort. Based on this, we advance that physical effort modulates arousal which can, in turn, explain its effect on speed and accuracy of responses. This is the hypothesis we plan to test in this study. In our previous work, we reported that larger physical effort induced shorter reaction times, poorer accuracy and lower psychophysical performance in a perceptual decision-making task. We advance that SAT modulations under physical effort might be due to arousal induced by the effortful movements. Thus, the main hypothesis of this work is that physical effort alters pupil-linked arousal as well as modulating speed accuracy trade-off. In order to test this hypothesis, we used a random dot motion task in which we manipulated the response deadline and level of effort that is required to initiate and sustain sensory evidence. First, we checked whether effort influences SAT similar to a deadline manipulation, to reproduce our own previous results. Second, after confirming these results, we assessed whether effort changed baseline pupil diameter which is a marker of tonic arousal and checked whether the baseline pupil diameter correlates with speed and accuracy. In specific, we predicted larger baseline pupil sizes with larger physical effort.

2. Methods

2.1. Participants

Twenty participants were recruited via e-mail invitations through the database of the Center for Brain & Cognition (Universitat Pompeu Fabra). The number of recruited participants was decided before the data collection, based on our previous work with the same paradigm (Chapter 2.2.) and considering the potential data losses due to pupil recording. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of motor problems related to use of their left hand, arm and wrist. They all signed an informed consent form and a data privacy form. The experiment was approved by an institutional ethical committee (CIREP, Universitat Pompeu Fabra) and all methods were performed in accordance with the relevant guidelines and regulations. According to our data inclusion criterion decided a priori, after the first block of trials (125), we assessed the participant's performance. If the participant had not reached at least 75% in the easiest stimulus level (52% dots moving coherently), we did discontinue the data collection. With this criterion, 12 participants completed the whole experimental session of 2 hours.

2.2. Apparatus

The experiment was conducted in a dimly lit room. Visual stimuli were presented on CRT monitor (Sony Multiscan G520; refresh rate 60 Hz; 1024 × 768 pixels) which was placed 65 cm away from the participant's head (as it rested on a chinrest). Seat and chin-rest height were adjusted at a comfortable position for each subject. To measure effort, a hand dynamometer (Vernier HD BTA, with Arduino USB adaptor) was used. To record pupil size during the experiment, Tobii x120 eye-tracker was used. Stimuli and experimental scripts were programmed in Matlab, PsychToolBox.

2.3. Visual Stimuli

In this experiment, we used the exact same parameters and process to produce Random Dot Kinematogram (RDK) stimuli with our previous experiment (Chapter 2). There were 5 levels of logarithmically spaced dot coherence; .032, .064, .128, .256, .512. The overall stimulus characteristics and algorithm have been replicated from the classical version of RDK (Gold & Shadlen, 2003). The stimuli color was white and the background of the presentation was dark grey.

2.4. Task and Effort Manipulation

The main task in the experiment was to report the direction of motion, which a portion of dots were coherently moving towards. In order to study the effects of deadline imposition and physical effort, we used two deadline conditions (4s and 1.5s) and three effort conditions (No Effort, Low Effort, High Effort). No Effort condition served as a baseline situation which resembles the common version of a perceptual task with passive observation of stimuli and response by pressing a button. A typical trial started with a white fixation cross presented at the centre of the screen and after a fixed delay (calculated per subject from the mean duration to initiate trials in an effort block) the stimulus appeared. The participant could respond until the deadline (4s or 1.5s) by pressing left or right arrow keys with their right hand. If no key was pressed until the deadline, a yellow fixation cross appeared as a feedback.

Yellow cross indicated an invalid trial and those trials were repeated at a random time later in the block. If a subject gave a correct answer, the feedback cross was in green and if it was an incorrect answer, it was in red. This feedback cross appeared for 1.5 seconds. After that, a new trial started with presentation of a white fixation cross.

In Effort conditions, the trial structure was identical except for the force application. After the white fixation cross was presented which indicated the beginning of a trial, participants had to squeeze the hand dynamometer with their left hand. After the required level of force was reached, the stimulus appeared on the screen and remained as long as the hand press force was above the required force level. If the force intensity fell below the threshold, stimuli disappeared and a yellow feedback fixation was presented. As with the invalid trials due to no response, these trials were also repeated later during the block. Similar to the No Effort condition, green or red feedback crosses has been used to indicate correct and incorrect responses, respectively.

2.5. Procedure

Eye-tracker calibration

We needed to ensure if the participants’ eyes could be tracked effectively by the device. In order to do that, we administered a short calibration procedure (with a custom Matlab code) which involved presentation of markers on the screen and asking participant to follow the shape with their gaze. This took 2 minutes in total. Calibration process was successful in all participants.

Effort calibration

In order to calculate the required force levels for the effort conditions of the experiment, we measured the Maximum Voluntary Control (MVC) of each subject before the session. The participant was asked to press the dynamometer as hard as they can, three times in a row. Then, we took the average of these values as MVC for that participant. We took 10% and 25% of MVC as required force thresholds for Low and High Effort conditions, respectively.

Experiment

Each participant completed a training session which consisted of 15 trials, to familiarize with the task and incorporating hand pressing. Main purpose of the training was to help participants get used to the incorporation of hand press and overall timeline of trials. Therefore, we only used the upper 3 levels of stimuli to help ease the learning. The training process was repeated if the participant had not reached 70% accuracy. If the participant did not reach the required performance (70% accuracy) after 3 training sessions, we still proceeded to the first block of the experiment just in case they can learn the task during the first block. However, in first block if the participant could not perform at least 75% in the highest coherence, we finished the experiment and not continued with the rest of the blocks. There were 6 blocks in total which were assigned in random order. In each block, there were 25 trials per coherence which make 125 trials in a block and 750 trials in whole experiment.

3. Data Analysis

Behavioural Analysis

Analysis of the experimental data required mainly assessing speed and accuracy of the data. For group comparisons, we used ANOVA if adequate assumptions for analysis of variance were not violated. We also conducted per participant linear regressions with the factors; effort, deadline, and coherence. To calculate psychophysical thresholds, we fitted psychometric curves to the participant data. We used GLM with logit link function to fit the curves. Analyses have been done with custom made Matlab scripts.

Pupilometry Analyses

We followed a pre-processing pipeline which involved data cleaning, interpolation for missing values and smoothing. Raw pupil data usually involves abnormal erratic values that are due to blinks, thus an important step in pupil data cleaning is detecting blinks and correcting them (Knapen, et. al., 2016, Mathot, 2013). Other sources of artefacts in raw pupil data are periods with no data; either due to eye-tracker cannot resolving the pupil size from camera image or certain head movements of the person (Mathot, et. al., 2016). For both blinks and missing data the common treatment is to apply interpolation. In line with the conventional pre-processing steps in pupillometry research, we identified blinks and missing data and then filled those by cubic-spline interpolation. We excluded trials which had more than 25% of data points interpolated. We then low-pass filtered the data (10 Hz). For these pre-processing stages, we used a built-in Matlab repository called PUPILS (link: https://gitlab.gbar.dtu.dk/heliaib/PUPILS-preprocessing-pipeline.git) which was developed by Relano-Iborra & Baekgaard (2020). The details of the algorithm and procedure is explained in their publication.

After the pre-processing, we normalized the pupil size values within subject by subtracting the mean pupil value and dividing it to standard deviation. To make data ready for the analysis, we aligned the pupil time series with respect to onset of trial and calculated the baseline pupil size as the average normalized pupil size for the 500 ms time window prior to effort production and stimulus onset. The baseline value is subtracted from the time series data to assess the dilation and other phasic components of the pupil time series data. In one participant, majority of the trials (109 out of 125) from one condition did not have any recorded signal (possibly due to removing the head from the chin-rest), therefore we excluded that participant's data from pupil analysis data pool. We ended up with N=11 for all the pupil analysis.

3. Results

3.1. Reality Check: Force Exertion in Low and High Effort

Participants could potentially exert larger than necessary force in the Low Effort condition which might have caused two effort levels in our experiment to be similar, defeating the purpose of the manipulation. We set to ensure that the effort conditions effectively set a minimum for Low and High Effort by checking the average forces applied in the two conditions. As can be seen in Figure 1, Low and High Effort conditions were clearly separated in terms of their average force levels. We also conducted paired-samples t-tests to compare the average forces applied in the two effort conditions. The result showed that in both 4s and 1.5s deadline conditions the average force applied in each condition was significantly different (t(11) = -10.1, p < .001, Cohen's d = -2.9 and (t(11) = -6.4, p < .001, Cohen's d = -1.85) throughout the average duration of the trial.

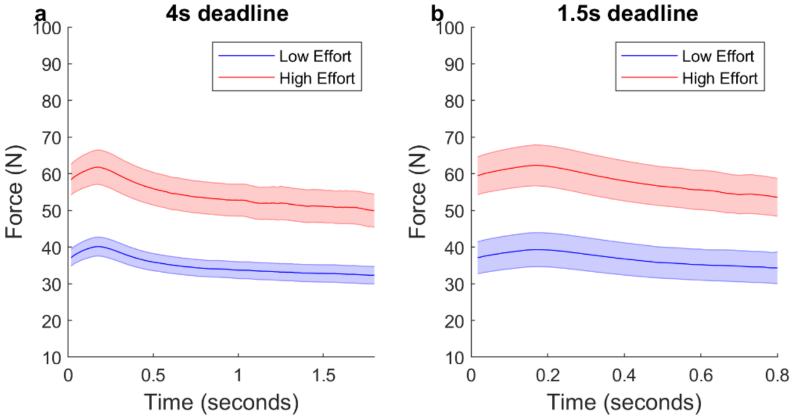

Figure 1. a. Average force profile in 4s deadline condition from all participants. Red trace indicate High Effort condition and Blue trace indicates Low Effort condition. Shaded area is standard error of mean S.E.M. **b.** Average force profile in 1.5s deadline condition from all participants. Red trace indicate High Effort condition and Blue trace indicates Low Effort condition. Shaded area is standard error of mean S.E.M.

3.2. Speed and Accuracy

In order to test if deadline and effort changed speed of decisions, we conducted an analysis on the mean reaction times per condition with one-way ANOVAs (a Shapiro-Wilk test of normality showed that the normality assumption was not violated, $p > .05$). To test for the deadline and effort effects on RT, we proceeded with repeated-measures ANOVA with deadline and effort as independent variables over RT. The results showed that both deadline and effort had significant effects on RT ($F(1,11) = 89.5$, $p < .001$, $\eta^2 = .78$ and $F(2,22) = 19.2$, $p < .001$, $\eta^2 = .06$, respectively) in the expected direction. To look further at effort-induced RT speed up in each deadline condition, we conducted two separate one-way ANOVAs. We found that effort reduced RTs significantly in both 4s (No Effort = 2.05s, Low Effort = 1.89s, High Effort = 1.52s, $F(2,22) = 23.1$, $p < 0.001$, $\eta^2 = .7$, Figure 2a) and 1.5s (No Effort = .9s, Low Effort = .88, High Effort = .83, $F(2,22) = 3.4$, $p < 0.05$, $\eta^2 = .24$, Figure 2b) deadline conditions.

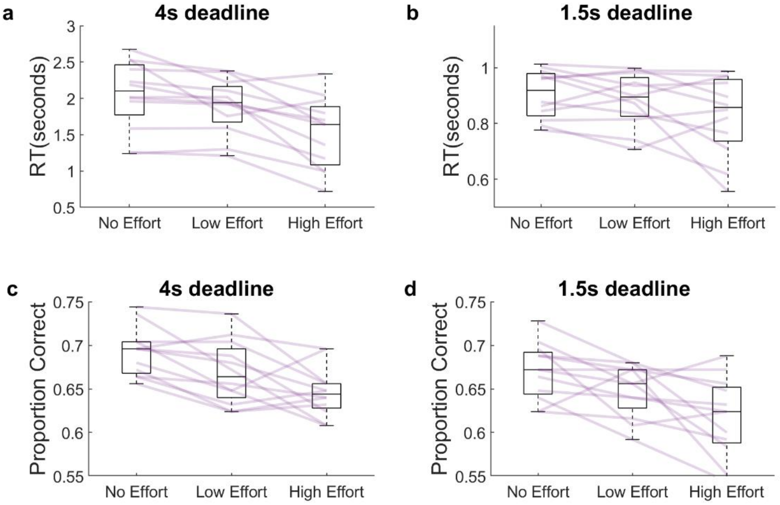

Figure 2. Box plots of average RT and Proportion of Correct responses. Horizontal lines indicate median values and purple lines

are each participant’s average values. **a**. Average Reaction Times from 4s deadline conditions. **b.** Average RTs from 1.5s deadline conditions. **c.** Average proportion of correct responses from 4s conditions. **d.** Average proportion of correct responses from 1.5s conditions.

The above analyses focused on averages for each deadline/effort condition and therefore did not take stimulus intensity (coherence) into account. As task difficulty has a big influence on RT, we conducted Linear Regression analysis to predicted RTs from Deadline, Effort, Coherence and their interactions. We fitted regression models for each participant separately, and then extracted each coefficient of the regression model. Then, we assessed the average coefficient values from all participants whether they differed significantly from 0. We found that Deadline, Effort and Coherence coefficients were significantly different from 0 (Figure 3). When it comes to interactions, Deadline*Effort, Deadline*Coherence and Deadline*Effort*Coherence regression coefficients were significantly different from 0 (Figure 3). To have a better grasp of the interactions, we plotted RT as a function of coherence in each Effort condition and each Deadline separately (Figure 4). All in all, RTs became faster at higher coherence across the board. This coherence effect was more steep with the long deadlines (can be seen in Figure 4, each panel). In addition, there was an overall reduction in RTs specifically for the longer deadlines. The steeper effect of coherence and overall reduction of RTs with effort was constrained to the longer deadlines, indicating that shorter deadlines did not leave much room for speeding up. Lastly, the RT difference between 4s and 1.5s. deadline conditions were larger for No Effort condition, compared to effort conditions. (Figure 5). It is clear that the effect of coherence on RTs is modulated both by deadline and effort.

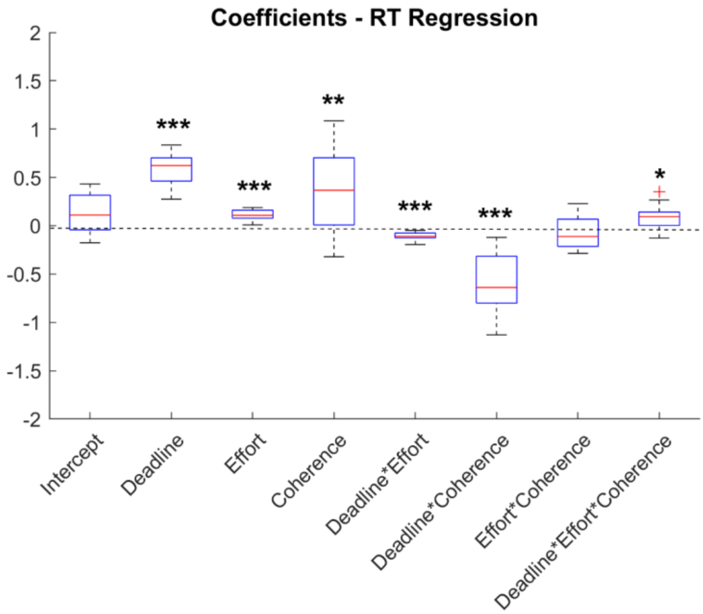

Figure 3. Average coefficients from per participant linear regressions to predict RT with Deadline, Effort, Coherence and their interactions. *** = p < .001, ** = p < .01, * = p < .05)

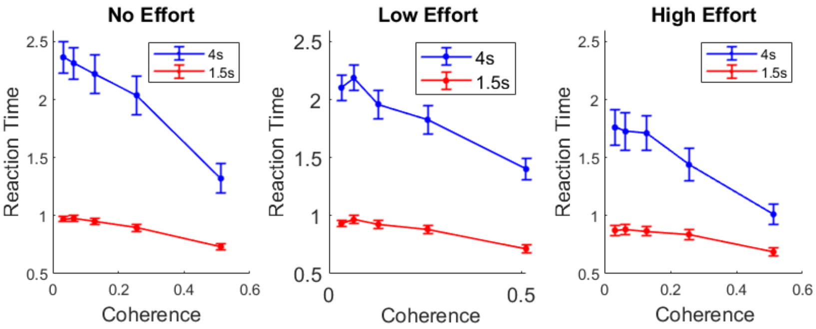

Figure 4. Average RT (y-axis) for each Coherence (x-axis). 4s and 1.5s deadline conditions are represented in blue and red lines respectively.

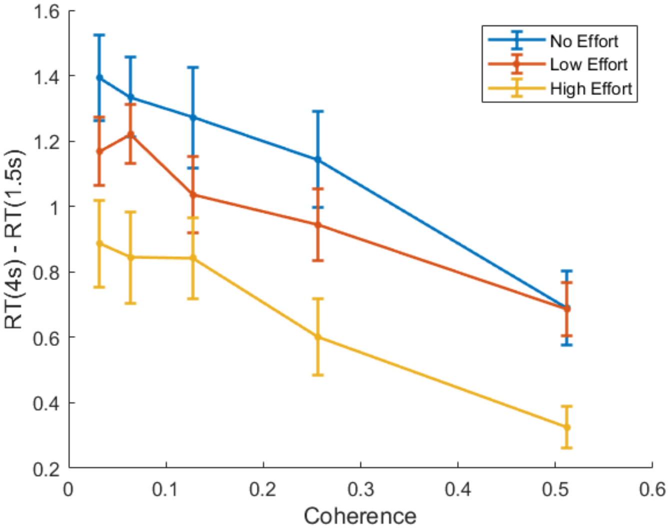

Figure 5. The difference between average RTs in 4s and 1.5s deadline condition. x-axis indicates the Coherence and each line belongs to a different effort condition.

After showing that effort speeded up decisions, we moved on to inspect whether effort also has an influence over accuracy. Similar to the RT analysis, we ensured that accuracy estimates did not violate the normality assumption (Shapiro-Wilk tests, $p > .05$). We conducted two-way repeated measures ANOVA with the Deadline and Effort as factors over Accuracy. The results showed that both deadline and effort had significant effects on accuracy ($F(1,11) = 20.4$, $p < .001$, $\eta^2 = .13$ and $F(2,22) = 18.7$, $p < .001$, $\eta^2 = .4$, respectively). To check the effect of effort in both deadline conditions, one-way ANOVAs ran on each deadline condition separately showed that effort led to lower accuracy in both 4s (No Effort = .69, Low Effort = .67, High Effort =.64, $F(2,22) = 10.1$, $p <$

0.001, $\eta^2 = .47$, Figure 2c) and 1.5s (No Effort = .67, Low Effort = .65, High Effort = .62, $F(2,22) = 12.4$, $p < 0.001$, $\eta^2 = .53$, Figure 2d) conditions. After assessing these accuracy effects with condition means, we proceeded to a regression analysis including Coherence as a factor as well as deadline and effort. We built Logistic Regression Models per participant to predict Choice (correct or incorrect) from Deadline, Effort, Coherence and their interactions. We extracted coefficients from each participant and then checked with two-way t-tests if they were different from 0. We found that only the coherence coefficient was significantly different from 0. Thus we see that, trial by trial prediction of choice accuracy was not robust with the current dataset. Although, effort had an influence over group averages in accuracy, trial-by-trial fluctuations could not be confirmed with individual logistic regression analysis. Moreover, since we used a constant stimulus protocol, as an alternative to directly analyzing proportion of correct responses we also assessed performance by fitting psychometric curves to extract perceptual thresholds.

3.3. Psychometric Threshold

For each participant and each condition, we fitted a curve for the proportion of correct responses across coherence levels by using a GLM with a logit link function. The coherence value that gives 75% performance was used as the threshold value. If deadline and effort induce any in motion perception decisions, we expected to see a difference in these thresholds. To test this prediction, we conducted two-way repeated measures ANOVA with deadline and effort as independent variables and threshold as a dependent variable. The results showed that both deadline and effort significantly modulated threshold (F(1,11) = 29.9, $p < .001$, $\eta^2 = .17$ and F(2,22) = 17.9, $p < .001$, $\eta^2 = .39$, respectively). The interaction effect on the other hand was not significant (p = .7). In general, effort lowered performance (increased the threshold) both in the 4s (No Effort = .19, Low Effort = .24, High Effort =.25) and 1.5s (No Effort = .22, Low Effort = .27, High Effort =.29) deadline conditions. To better grasp the changes in RT and performance together, we plotted average RTs and Thresholds for each condition in Figure 4. It can be clearly seen that both in the 4s and 1.5s deadline, effort reduces both RT and performance (Figure 6).

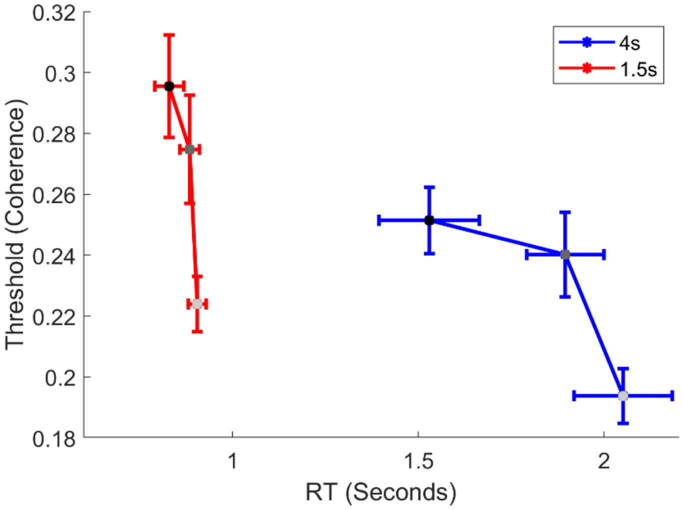

Figure 6. Average RT (x-axis) and Threshold (y-axis) for each condition. Purple line indicates 4s deadline condition and Yellow line indicates 1.5s deadline condition. The shade of the points represents effort condition, light grey: No Effort, dark grey: Low Effort and black = High Effort. Error bars represent S.E.M.

Threshold as obtained from the psychometric curves can inform about the level of performance in motion perception. The other information that we can gather from psychometric curves is the slope of the curves which indicate the precision/sensitivity of detecting motion. Thus, we analyzed if effort and deadline induced significant changes on the slope of psychometric curves. We conducted a repeated-measures ANOVA similar to the previous analysis. We found that both deadline and effort had a significant effect on slope ($F(1,11) = 11.5$, $p = .049$, $\eta^2 = .07$ and $F(2,22) = 16.7$, $p < .001$, $\eta^2 = .21$, respectively). Specifically, in Long Deadline condition the slopes were generally higher. Within each deadline condition, No Effort conditions had a higher slope than the effort conditions (4s deadline, No Effort = 7.7, Low Effort = 5.7 , High Effort = 6.1 and 1.5s deadline, No Effort = 6.4 , Low Effort = 5.4 , High Effort = 5.3). It will be discussed later that, at least according to the effect size, the effect of deadline effect was smaller than the effect of effort.

3.4. Tonic Pupil Size

Tonic pupil size is an indicator of baseline arousal levels and is measured from a period that precedes task-related stimuli. Based on our hypothesis that physical effort induces arousal changes, we predicted larger baseline pupil sizes in higher effort conditions. To test this prediction, we extracted the baseline pupil size by averaging the pupil size during the 500ms pre-stimulus and pre-effort period. After averaging the normalized baseline values for each participant, we conducted a two-way repeated measures ANOVA to check if deadline and effort induce significant effects on the baseline pupil sizes (the normality assumption to was not violated, Shapiro-Wilk test, $p > .05$). The results showed that effort had a significant effect on baseline pupil size ($F(2,20) = 8.75$, $p < .001$, $\eta^2 = .35$), but deadline did not ($F(1,10) = .22$, $p = .6$). Looking separately at each of the two deadline conditions, we confirmed that effort increased baseline pupil size in both, 4s (No Effort = -.26, Low Effort = -.17, High Effort = .2, $p = 0.02$, $\eta^2 = .34$), and 1.5s (No Effort = -.47, Low Effort = -.05, High Effort = .15, $p < 0.001$, $\eta^2 = .56$) deadline conditions. Thus, we confirmed our hypothesis that higher effort levels induce a larger tonic arousal and this could potentially drive physical effort's influence on speed and accuracy.

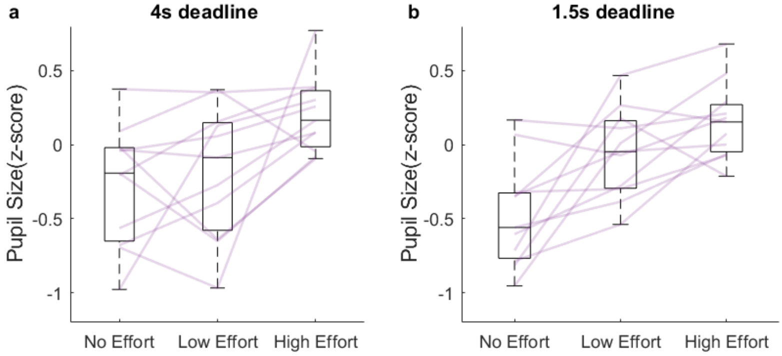

Figure 5. Box-plots of normalized baseline pupil sizes for the 4s deadline condition (**a.**) and for the 1.5s deadline condition (**b.**) at each effort level. Purple lines indicate individual participant means.

3.5. Tonic Pupil Size and Effort-related SAT Effects

As it is important for us to test whether effort-induced changes in speed and accuracy of responses can be explained by arousal, we looked at how accuracy and RTs correlate with baseline pupil size. Since baseline pupil size did not show significant differences between 4s and 1.5s deadlines (Results 3.4), here we pooled the data from the two deadline conditions and focused on comparing effort conditions. We found that average pupil size across participants for each effort condition correlated very strongly with proportion of correct responses for each condition (r = -.99, p = .02, Figure 6a) and the correlation was significant. Furthermore, the correlation between pupil size and RT was also significant (r = -.98, p = .04, Figure 6b).

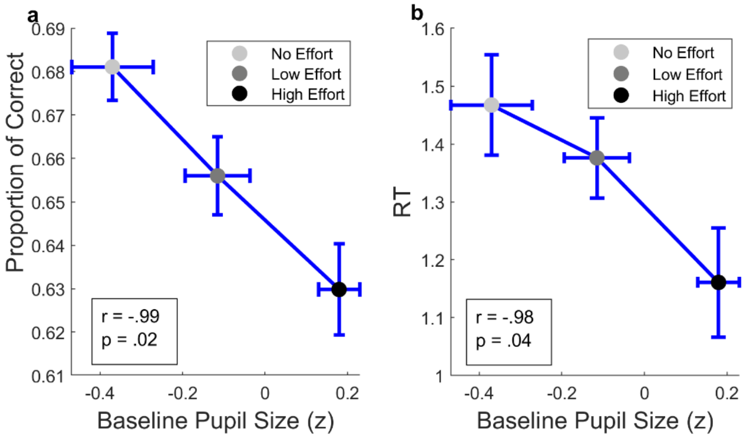

Figure 6. a. Average normalized baseline pupil sizes (x-axis) and proportion of correct responses for each effort condition. Error bars represent S.E.M across participants. Correlation coefficient between pupil size and proportion of correct responses is shown in text box left bottom corner. **b.** Average normalized baseline pupil sizes (x-axis) and RTs for each effort condition. Error bars represent S.E.M across participants. Correlation coefficient between pupil size and proportion of correct responses is shown in text box left bottom corner.

After addressing the correlation between baseline pupil size and proportion of correct responses with the pooled data from all subjects, we also checked the same correlation per participant. We collected each correlation values per participant and ran t-tests to check if the correlations were significantly different from 0. It turns out that the correlation between baseline pupil size and proportion of correct responses across effort conditions were significant (average r = -.52, range = [-.99 .2] p = .005). Four out of 11 participants showed a significant correlation individually. Similarly, the correlation between baseline pupil size and RT was also significant (average = -.58, range = [-.95 .4], p = .03), and three out of 11 participants had significant correlation individually. We checked the across participant variation (see Figure 7) in the range of correlation values for baseline pupil and the two behavioural measures (proportion correct and RT). Although, the distribution of these variabilities indicated that there were some participants who did not show a strong correlation between pupil size and RT, overall, baseline pupil size correlated strongly and negatively with speed and accuracy of responses. Thus, it is plausible to conclude that effort-related changes in SAT can be at least partially due to higher arousal.

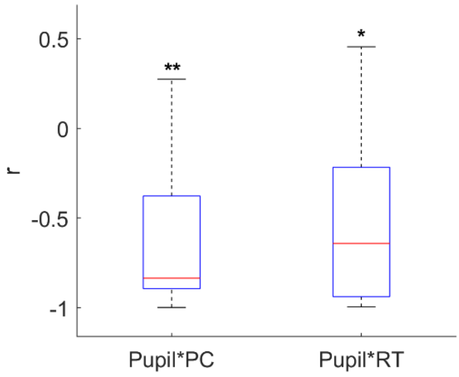

Figure 7. Box-plot for correlation coefficients for Baseline Pupil with Proportion of correct responses and with Reaction Times. ***: p < .001, *: p < .05.

3.6. Pupil Dilation Dynamics

Although we did not have a specific hypothesis about pupil dilation during stimulus processing, significant support in the literature posits that phasic pupil dynamics are highly linked to tonic levels of arousal (de Gee, et. al., 2020, van Kempen, et. al., 2019). Namely, when there is a large baseline pupil size, it is likely to see less task-evoked dilation. Therefore, it is difficult to interpret phasic changes when there are systematic changes in baseline pupil sizes, which is the case in our results. First, we wanted to confirm if baseline pupil size really predicted the pupil dilation in comparison to other factors. Therefore, we fitted linear regression models for each subject to predict pupil dilation (maximum baselined pupil size measured during a trial) from Deadline, Effort, Coherence, Baseline Pupil Size and their interactions. We included all trials with valid pupil data into the analysis. We found that, in all participants, baseline pupil size was a significant predictor of phasic pupil dilation (mean = -.57, range: [-1.2 -.17], $p < .05$). It is crucial to point out that in all subjects, the coefficient for baseline pupil size was negative, which confirms the results in the literature on the notion that there is an inverse relationship between tonic and phasic pupil size. After fitting regression models and obtaining coefficient estimations, we ran t-tests to test for group effects. We found that Baseline Pupil Size was the only main term that was significant at predicting pupil dilation (Figure 8). The Coherence*Baseline interaction coefficient was also significantly different from 0 ($p < .05$). This makes sense as usually phasic changes in pupil during a cognitive task rely a lot on the cognitive effort which in our case boils down to stimulus difficulty. All in all, we can confidently say that pupil dilation was strongly influenced by baseline pupil size, and therefore any strong modulation as a function of other experimental factors was muffled.

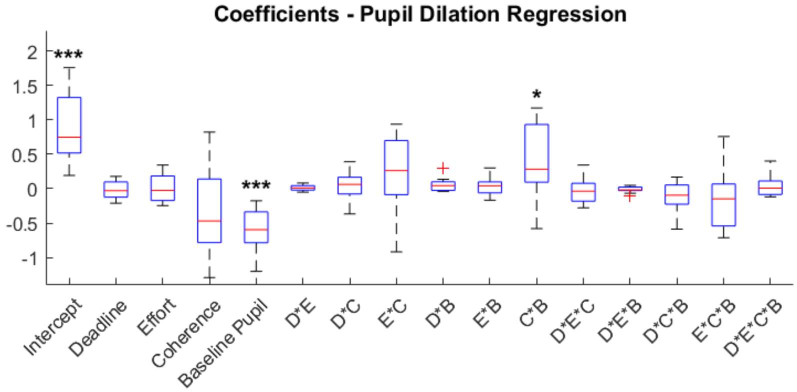

Figure 8. Coefficients from Regressions to predict pupil dilation. Bars with asterisk(s) indicate that the coefficients across participants are significantly different than 0. ***: p < .001, *: p < .05.

4. Discussion

In this work, our aim was to demonstrate (1) that physical effort can induce urgency changes, with an impact on shortening reaction times and reducing accuracy similar to deadline impositions and, (2) that arousal changes resulting from the physical effort follows these SAT regulations, namely increased tonic arousal with larger physical effort. Our results supported both of our premises and corroborated the results from our previous work. Similar to that work (Ozbagci, et. al., 2022) here we also reported RT speed up and performance reductions as a function of physical effort. Then, we also showed that in accordance with our hypothesis, higher physical effort conditions exhibited larger tonic arousal, measured by baseline pupil sizes. There are already works in the field reporting the link between physical effort and arousal (Zenon, et. al., 2014), yet this is the first study we know which shows these effort-related arousal adaptations in relation to perceptual decision making. Our task involved making visual discrimination in which the evidence accumulation was contingent on physical effort. In a way, physical cost of information sampling was manipulated. Interpreted this way, our work concludes that effort of sampling information is an important factor in the speed-accuracy trade-off during perceptual decisions and effort-induced arousal alterations can be the key mechanism behind it.

As discussed in the introduction, arousal is a brain-wide state that impacts a variety of processes including decision making and perception (Aston-Jones & Cohen, 2005). Similarly, global gain mechanisms driven by arousal have suggested to have a specific role in optimal decision making (Niyogi & Wong-Lin, 2013). One obvious mechanism of optimal decision making is regulating speed and accuracy of responses (Murphy, et. al., 2014). Thus, it seems important to elaborate on the urgency-arousal interaction. From the brain anatomy point of view, the main candidate brain correlates of urgency are, on the one hand activity in the striatum (van Maanen, et. al., 2016), and on the other hand noradrenergic release that originates in LC and cholinergic release controlled by basal forebrain (Jones, 2004, Reimer, et. al., 2016, Lee & Dan, 2012). LC has many projections across the brain and striatum is one of the areas that has a primary connection and similarly cholinergic release impact the whole cortex. Therefore, the interaction between

LC and striatum can be how arousal contributes to urgency dynamics and therefore can explain (at least partially) SAT modulations (Steinemann, et. al., 2018). This being said, the common way to study urgency is imposing a temporal deadline on responding (Heitz, 2014). In the present experiment, we also introduced a short deadline to impose urgent decisions. And as we did in our previous experiment, we found that physical effort induced a very similar behavioral output as deadline manipulation in terms of lower RTs and accuracies. Following the results of both studies, we can claim that urgency is a mechanism that takes both time-based and effort-based costs into account.

Our claim about urgency carrying both the time-based and effort-based constraints does not necessarily indicate that these two types of urgency-inducing variables (time and effort) have the same mechanistic relationships within the brain. In the present experiment, we showed that tonic arousal is increased with effort intensity and correlated negatively with accuracy and RT. However, we could not find an effect of deadline on tonic arousal, albeit it induced clear differences in both RT and accuracy. Effort related changes in SAT may be mediated or heightened by arousal and LC, while pure deadline impositions can be mediated by other structures for instance that related to processing of time. In fact, there are plenty of researchers who supported that speed of responses in decision making tasks are mediated by timing ability of individuals (Frazier & Yu, 2008, Miletic & Van Maanen, 2019, Balci & Simen, 2016). Another crucial point of different urgency mechanisms is that there are already disputes in the literature about the shape of the urgency signal (Hawkins. Et. al., 2015, Murphy, et. al., 2016). Depending on different experimental structures, some data could be explained better with growing urgency signals (continuously increasing signal throughout the trial which pushes the agent toward the decision bounds), whereas other studies found static urgency (a criterion set from the beginning of a trial which does push the decision to be made when a certain time point is reached) to better explain experimental data (Steinemann, et. al., 2018). Since, in this work we did not used a mechanistic model such as DDM or Urgency Gating Model to fit our data, we cannot claim whether our data favors one over the other. However, it is highly favorable if in the future such tests would be made to compare time-based and effort-based urgency.

Our main interpretation about effort-related arousal adjustments and observed SAT effects attributes a role to arousal in mediating the speed and accuracy changes under effort. However, an alternative explanation could be that arousal effects and observed behavioral effects are two independent mechanisms that physical effort has induced. It is hard to refute this explanation, yet considering the literature on how tonic pupil size influences perceptual decision making, it is unlikely that the arousal changes would not influence speed and accuracy. For instance, Park, et. al., (2021) have conducted an experiment that studied visual search under different physical effort regimens and found that due to heightened arousal levels, visual search was faster and more subject to errors under large loads of physical effort. Similarly, Murphy, et. al., (2014) have studied perceptual decision making with the same random motion task as in our study and reported that in trials with higher pupil size, the performance was more variable and included more errors. They concluded that high tonic arousal might lead to larger noise and less efficient evidence accumulation. Under the light of these evidences, it is not too speculative to assume a specific role of arousal in relation to faster and less accurate decisions under high physical effort.

As explained above, our hypothesis depended on tonic arousal and physical effort interactions, and we did not have specific predictions about phasic dynamics in pupil size. It is known that phasic dynamics in pupil-linked arousal is highly and negatively correlated with baseline pupil sizes (Gilzenrat, et. al., 2010, de Gee, et. al., 2014, van Kempen, et. al., 2019, This intuition indicates that when there are baseline changes in pupil size, it is important to control if this pattern explains the phasic pupil changes before interpreting any phasic changes due to any experimental variable. We reported in results section that baseline pupil has significantly predicted the phasic changes. Despite our main hypothesis regarded the tonic changes in arousal, it is important to note that there are many other studies which reported changes in phasic arousal due to urgency (Murphy, et. al., 2016, van Kempen, et. al., 2019). It is therefore difficult to say that only phasic or tonic changes in arousal are related to urgency and accuracy of responses. Both might be at play, especially considering the tight coupling between the two. To summarize, we are concluding that effort-related changes in SAT are attributable to tonic arousal whereas other mechanisms still might be at play.

In summary, in the present study we showed that physical effort that is contingent on evidence accumulation induces urgency, similar to that typically seen due to deadline impositions. Furthermore, these effort-related urgency effects are captured by tonic arousal, measured by pupil sizes. However, tonic arousal did not show changes as a function of deadline which indicates that time-related urgency might have different mechanisms. Urgency takes both time-based and effort-based costs into account in order to optimize decision process in terms of reward rate. Yet, the functional and mechanistic connections within the brain for each type of urgency inducing situations are possibly different. This is the first experimental study which looked at the coupling between effort-related urgency and arousal. Therefore, more can be discovered via future research that investigates in detail what are the other potential dynamics which control effort-related urgency.

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3. GENERAL DISCUSSION

The overarching goal of this thesis was to enhance the understanding of the interactions between decision making and action, especially in cases when the decision takes place meanwhile an action must be executed. Such situations would include, for example, those in which information sampling that is relevant for the choice involves acting. These situations are common in everyday life behaviours, yet they have been investigated only superficially.

We had a theoretical affinity towards embodied decision making in the development of research ideas and designing the experiments. Thus, generating new and relevant hypotheses based on the current knowledge was at utmost importance for this dissertation. Each study had tests about various sub-questions, and we can summarize the main hypotheses corresponding to each of the studies as follows:

1. Actions related to decision making and actions related to sampling of information are subject to online interaction.
2. Physical effort imposes urgency in decision making similar to time-constraints.
3. Physical effort alters arousal as well as modulating speed and accuracy trade-off.

In this last chapter, I will summarize the results we obtained in response of the tests performed on these hypotheses, as well as discuss the overall implications of the three studies with respect to the most relevant findings and theory in past literature.

3.1. Interactions between sampling actions and choice related actions

The results from Chapter 2.1. indicate that movements to sample information and movements to execute choices are in continuous interaction. The key aspect of the study was that sampling of information was required (at least in some of the conditions), and that sampling actions involved the same effector, the hand, as the choice response. The main hypothesis was that actions related to decision making and actions related to sampling of information interact during the course of a decision. To test this hypothesis, we implemented a mouse movement task in which upward movements helped to gain information about the visual stimulus whereas the horizontal movements were used to report the choice. By looking at the hand movement trajectories from this task, we found that even during the active sampling stage (upward movement) there were significant choice related movement components (horizontal deviations).

Another important finding was that not all trials have exhibited sampling actions. In some trials, participants rather remained stable at the initial location and acted only to go and respond. This bimodality in behavioural responses, some sampling and choosing at the same time (sampling responses) and others sampling first then acting (non-sampling responses), implies that a sub-decision took place at the very beginning of a trial on whether to sample information or not. Further supporting the presence of an initial sub-decision, we observed that in sampling trials participants initiated the movement significantly earlier than in non-sampling trials, in which they waited longer at the initial location. We interpret this waiting period as if participants were relying on internal evidence accumulation instead of an active one. This highlights the flexibility of types of decision making strategies humans can resort to, in adaptation to external and internal conditions. In certain situations, when there is a stronger need to accrue information, sampling movements are executed earlier and therefore allow for more nuanced embodied interactions. However, there are also cases which resemble more a serial decision making process; first deliberating internally and then executing the movements to respond. Therefore, this is exactly why we do not support the position that all decisions are embodied across the board. Yet, most ecological situations require moving to sample more information and in those situations decisions and actions interact in a continuous fashion. This is in line with the recent theoretical stances within embodied choice framework (Gordon et. al., 2021) that instead of replacing classic serial view of decision making, we need to understand its limits and when it is replaced with parallel action-decision dynamics.

3.2. Movement trajectories reveal decision making dynamics

Overall, our work in Chapter 2.1. contributes to a body of studies which study decision-making by analysing movement trajectories. In recent years, there has been an increase in the number of studies reporting novel movement trajectory experiments, so that during the time of this thesis, new articles have been published with a similar approach to ours (Kurtzer et. al., 2020, Michalski et. al., 2020, Pierrieau et. al., 2021). For example, Cos et. al., (2021) have conducted a study in which they assessed reaching movement trajectories during a decision making task and found that after the movement initiation participants were still carrying on decision process which was manifested with changes of mind in the trajectories based on cost and reward associated with options. Thus, their work also extends our knowledge on decision making during action. Furthermore, Michalski et. al., (2020) studied movement trajectories during a decision making task in which subjects needed to track a target with their movements and switch to a new target that appears if they would like to. They found that the switching to a new target depended on the distance of the new target, in a way that switching costs were influencing the rate of switches. Although these two studies and ours too had different paradigms and addressed different questions, they all support the idea that movement trajectories can reveal underlying decision dynamics.

3.3. Physical effort alters decision making

After concluding that the actions to sample information are integrated in the decision process, we focused on the effort of actions that are needed for information accumulation and whether it has an effect on decisions. In the second empirical study presented in this thesis (Chapter 2.2.), we studied whether physical effort influences speed and accuracy of responses. As we hypothesized that decision urgency is modulated both by time-constraints and effort-constraints, we compared performance in a perceptual decision making task under different effort and duration schemes. In particular, the experiment in Chapter 2.2 (and Chapter 2.3) introduced effort-contingent evidence sampling, so that effort exertion did not just occur during the decision making process, but participants had to exert effort in order to obtain decision-relevant evidence. The results showed that increased physical effort led to a speed up of reaction times and reduction in choice accuracy, similar to speed-accuracy modulations when shortening response deadlines. This behavioural result was also replicated with a follow-up study which is presented in Chapter 2.3. Thus, we are safe to conclude that effort induces changes into speed and accuracy trade-off.

There are already studies which reported that effort influences decision making (Cos, 2017, Morel et. al., 2017, Marcos et. al., 2015). For example, it is reported that when the response action is costlier, subjects exhibit less changes of mind even if to correct their choices (Cos, 2017). This and similar results supported the idea that decision making requires balancing costs and rewards and effort is one type of such costs (Shadmehr, 2010). Although the aforementioned studies were able to point the effort and decision making interactions, their locus of study were limited to effort of actions that were required to report a choice. In contrast, here we coupled effortful action into the evidence accumulation stage. This effort-contingent evidence accumulation is a novelty of our paradigm and therefore posits our results into a novel place. We attempted to capture natural settings where actions are needed to be able to perceive and interact with the world. Our experiment tried to emulate these more ecologically valid situations within the limits of well-controlled lab experiments. So, building on the existing work on the effort and decision making relation, our work contributed the novel insight that effort, which is coupled with evidence accumulation, modulates decision making. After concluding that physical effort modulates SAT in a perceptual decision making task, we considered potential mechanisms that might have accompanied the effort-induced changes in decision making. Since effortful actions induce increases in arousal and high arousal is linked to modulations in variety of cognitive processes, we pursued a following study to check the arousal under physical effort in the context of decision-making.

3.4. Arousal is a key mechanism for effort-related SAT alterations

After the second study under this dissertation (Chapter 2.2.), we questioned the potential mechanisms that might mediate the effort-based modulations in speed and accuracy of decisions. As motor actions require energizing the body and the brain, they have a strong relationship with arousal (Kurniawan et. al., 2021). We intended to check whether pupil size would be modulated under effort and whether it correlates with speed and accuracy effects we observed. We have conducted a random dot-motion task, in which the subjects needed to press a hand dynamometer in three different levels of force in order to see the stimulus. We predicted to see larger arousal in larger effort conditions. The result of this experimental study showed that baseline pupil sizes had a strong interaction with the physical effort that the participants had carried on during the task. Specifically, in higher effort conditions, the baseline pupil sizes were larger which indicated a higher tonic arousal. Furthermore, we demonstrated that the tonic pupil size changes in each effort condition was negatively correlated with reaction time and proportion of correct responses. Thus, we confirmed our hypothesis that effort of actions during a decision making task modulate arousal levels and this correlates with the speed and accuracy of the responses. This result is in line with the recent studies which have highlighted the influence of arousal on decision making (Jepma & Nieuwenhuis, 2011, Murphy et. al., 2014, Naber & Murphy, 2019). For instance, Naber & Murphy (2019) have reported that large baseline pupil sizes were predictive of faster and less accurate responses. Following this, we found that in high effort conditions, the baseline pupil was larger and responses were faster and less accurate. Thus, the effort's influence on arousal might be a key contributor of SAT effects due to effort intensity. In fact, high tonic arousal is usually related to higher variability in decision making process and faster responses (van Kempen et. al., 2019, Zenon, 2019). In extension to situations outside classic decision making paradigms, large baseline pupil sizes were found to be correlated with mind wandering, exploration and distractibility (Gilzenrat et. al, 2010, Jepma & Nieuwenhuis, 2011, Smallwood et. al., 2011). To sum up, speed and accuracy modulations under effort-induced arousal that we report here might be a manifestation of this highly vigilant, variable and poorly focused state of mind under increased tonic arousal.

3.5. Open questions

As it is the case with the most scientific studies, our study leaves more open questions than the ones it answers. Although we reported rich continuous dynamics between action and decision in Chapter 2.1, we are aware of the fact that some decisions are abstract (not significantly connected with motor actions) and therefore are executed in a passive fashion. For instance, deciding what is your favourite meal or which class to take the next semester are examples to decisions that can be executed merely mentally without the need to move around in an environment. In fact, most of the studies in the history of decision-making field were about these passive decisions that rely on deliberation without strong coupling with the motor system. To build a strong scientific framework, embodied decision accounts must invest on understanding the boundaries between embodied and not embodied manifestations of decisions. Therefore, it is an open question that when given the flexibility, what makes an agent to carry on an embodied decision process versus a pure cognitive one.

In relation to our work in Chapter 2.2 and 2.3, there is an open question about the difference between effort and perceived effort. Despite we used an objective measure of force as a proxy of effort, there are works that show that perceived effort is not directly correlated with the mechanical cost of actions. Similarly, perceived effort of a task with the same external demand can change as a factor of fatigue (Iodice et. al., 2017). We did not specifically focus on the effect of fatigue and how it influences the effort-induced decision effects that we found. Future work can look for how fatigue can monotonically change the decision process under physical effort.

Again in Chapter 2.2 and 2.3, we proposed that urgency is a mechanism that tracks effort-based costs as well as time-based costs. In order to bolster this claim, model-based approaches can be utilized. Potential implementations of evidence accumulation models (DDM) or more recent urgency models (Urgency Gating Model) may help us differentiate what processes drive the effort-based alterations in choice behaviour (Ratcliff & McKoon, 2008, Thura et. al., 2012). Specifically, it can be tested whether effort induced SAT changes can be accounted by urgency modulations or general shift in decision bias or drift rate can explain them. These are important questions that we are not able to answer yet. In future, we or other research groups should carry on these much-needed applications.

3.6. Concluding remarks

Under this PhD thesis, we investigated decision making during an ongoing action with three novel experimental studies. After establishing that sampling actions and response actions can be executed simultaneously (Chapter 2.1), we moved on to a detailed study of how effort of actions contribute to decision making

(Chapter 2.2). Finally, we sought after whether arousal is a critical factor in effort-related changes in decision-making (Chapter 2.3). Although it may seem as if there is a leap between the first study and the latter two studies, they are highly connected conceptually. In all three experimental paradigms, we utilized an ongoing action while a decision was being made. Similarly, in all paradigms stimuli were contingent on motor actions. Overall, we researched the influence and dynamics of actions during evidence accumulation stage. This conceptual continuity is highly relevant considering the overarching conclusion of this PhD dissertation. Costly physical actions influence decision making both in terms of dynamic changes in shape of trajectories and in terms of speed and accuracy of responses that are reported.

Our work contributes to a field that is gradually getting more prevalent in the last decades. Despite the dualist idea of mind and body that dominated studies of cognition and brain for a very long time, we see a surge of embodied approaches that revisits the coupling between brain and body from various angles. Yet, there is still a lot to understand about the mechanisms and limits of embodied decisions. In their extensive review of the field, Gordon et. al., (2021) mentioned important considerations about studying embodied decisions. They emphasized that to be able to answer the specific questions about decision and action relationship, there needs to be novel task designs which are still as rigorous as well-controlled classic setups. We think that the body of work described in this thesis is a response to such a need in the field. In addition to presenting novel evidence in favour of action-decision interactions, we hope that our work promotes further questions and inspires further studies.

4. Bibliography

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