How urgency shapes motor behavior

A doctoral dissertation presented by

Fanny Fievez

Health Sciences Sector (SSS)

Doctoral School in Biomedical and Pharmaceutical sciences

Université catholique de Louvain (UCLouvain)

Brussels, Belgium

2023-2024

Acknowledgements

First of all, I extend my heartfelt gratitude to my two promotors, Professors Julie Duque and Ignasi Cos, whose invaluable advice, availability, support, and patience have been instrumental throughout the years of my PhD.

I am also deeply indebted to the accompanying committee and the jury members, including Prof. Frederick Verbruggen, PhD. Gérard Derosière, Prof. Vincent Van Pesh, Prof. Philippe De Timary, PhD. Caroline Quoilin, PhD. Alexandre Zénon, and Prof. Paul Cisek. Their insightful comments and constructive suggestions have significantly contributed to the refinement of this work. A special acknowledgment is reserved for my president, Prof. André Mouraux, whose kindness and unwavering support during the pivotal stages of my thesis were deeply appreciated.

My sincere thanks extend to all the collaborators who played a role in this project. Foremost among them are all members of the Coactions laboratory, including PhD. Thomas Carsten, PhD. Emmanuelle Wilhelm, PhD. Pierre Vassiliadis, PhD. Shiyong Su, PhD. Goldy Yadav, Thibault Fumery, Fostine Chaise, Clara Braconnier, and Mantosh Patnaik. Their feedback during lab meetings has been invaluable. Additionally, I am grateful to the CATL team, comprising PhD. Julien Lambert, Benvenuto Jacob, Christian Lebègue, and PhD. Cédric Lenoir, for their invaluable support (technical and moral) over the past five years. Special thanks are due to PhD. David Thura for his help on data modeling in the Tokens Task. I also extend my appreciation to the administrative team, including Leila Azzaz, Sandrine Wollanders, Cathy Friand, and Prof. Valéry Legrain (as president of the doctoral school), whose dedication and efforts have facilitated the smooth progress of the PhD. Furthermore, I am grateful to the students who participated in various experiments and contributed to the refinement of my theoretical knowledge, including Florian Paquet, Adrien Van Hees, Léna Schroeder, Claudia Danse, Eline Volders, Baptiste Waltzing, and Fanny Schannes.

Finally, I wish to express my profound gratitude to my friends and family for their steadfast support, particularly my husband Fabien Seiler, for his flexibility and above all to be my greatest pillar in this adventure.

List of abbreviations

$ANOVA_{RM}$	repeated-measures analyses of variance
BF_{10}	bayes Factor
BIS	behavioral inhibition system
CI	confidence intervals
CRT	choice reaction time
DD	decision duration
DDM	drift diffusion model
HSD	Tukey's Honestly Significant Difference
IES	inverse efficiency score
ITI	intertrial interval
k-distance	mean square error between data distributions of the model and actual data distributions
P(incl)	prior inclusion probabilities
P(incl|data)	posterior inclusion probabilities
PD	Parkinson's disease
PES	post-error slowing
RT	reaction time
SAT	speed-accuracy tradeoff
SRT	simple reaction time
STN	subthalamic nucleus
SumLogLR	sum of log-likelihood ratios
Ter	non-decision parameter
TMS	transcranial magnetic stimulation
UGM	urgency gating model
UPPS	short version of the UPPS-P Impulsive Behavior scale
Δ	deltas
η_P^2	partial eta-squared
%Correct	percentage of correct choices

Table of content

1. General overview

Every day of our lives, we make decisions to interact with our environment in a goal directed manner. Among these choices, the most critical ones are those related to survival, such as determining the path to procure food or to sidestep potential obstacles or predators. Notably, various authors have linked these life-threatening scenarios to contexts of heightened urgency. The rationale is clear: when faced with imminent danger, we need to react quickly (i.e., prompt decisions and quick movements are non-negotiable). In this thesis, I delve into the impact of urgency on human behavior, exploring this phenomenon along two main axes. In the study reported in Chapter 1, I concentrated on global adaptations of behavior to diverse urgency contexts. The primary aim was to investigate the existence of a common mechanism coregulating the speed of decision making and movement execution. Such process would inherently invigorate both aspects of behavior within high-urgency scenarios. In this work, we also tested the hypothesis that this default control mode can be overshadowed by other processes depending on task demands, sometimes leading to a dissociation of decision and movement speed, as reported in past studies. Then, in Chapter 2, the focus shifts to behavioral adjustments on a trial-by-trial basis. This examination seeks to determine if post-error adjustments are influenced by the urgency level at which subjects engage in the task. In summary, our results unveil a nuanced interplay of various mechanisms influencing decision making and movement execution. Despite their disparate operating levels, all these mechanisms align towards a singular objective: optimizing the rate of reward within a given context.

2. General introduction

2.1. Evidence accumulation models

For many years, cognitive psychology developed computational models in order to explain how we select actions to interact with our environment (Brown & Heathcote, 2005; Cisek et al., 2009; LaBerge, 1962; Laming, 1968; Ratcliff, 1978; Smith & Vickers, 1988; Stone, 1960; Usher & McClelland, 2001). In these models, decision making is described as a process of noisy accumulation of evidence: during deliberation, sensory evidence is accumulated until the total evidence in favor of one of the potential actions reaches a certain threshold, at which point the decision is made and the action is initiated (Gold & Shadlen, 2007; Hanks et al., 2014; Ratcliff et al., 2016). Following these models, the two main factors influencing the decisions are the **quality of sensory information available** in the environment and the **amount of information required** to select the action. By combining these two factors, models are able to provide an estimate of the time used for deliberation and the accuracy with which the decision is made (Cisek, 2006; Ratcliff & Smith, 2004). In this section, I will describe these accumulation models. First, I will focus on the basic principles, by summarizing the main variants found in the literature. Based on this summary, I will also discuss the two models I used for my PhD project. Second, I will consider how the models can explain behavior adaptations under urgency. To do so, I will specifically focus on studies looking at behavioral adaptations when decisions need to be made under time pressure. Importantly, behavioral adaptations can be observed at two levels: on the one hand, at a "macroscopic" level by looking at how subjects adapt their behavior according to the context in which they find themselves (i.e., **contextual adaptations**, as considered in Chapter 1), on the other hand, at a "microscopic" level

by looking at how subjects adapt their behavior from one trial to the next. Generally speaking, such trial-by-trial adaptations are particularly interesting following errors; in this context they are called **post-error adjustments** (as considered in Chapter 2).

Basic principles of accumulation models

Most models are used to explain decision making in experiments with two action alternatives. However, several variants exist in the literature (see Bogacz et al., 2006 and Ratcliff & Smith, 2004 for reviews). For example, models can differ in their evidence accumulation mechanism. Indeed, the accumulation can be computed through one or two accumulator(s); using one unique accumulator consists of transforming evidence into the probability of choosing one option over the other through integration (Cisek & Thura, 2022; Diederich, 2003; Ratcliff & Smith, 2004; Stone, 1960), whereas using two accumulators consists in having one capturing evidence for each option independently (Brown & Heathcote, 2005; LaBerge, 1962; Logan, 2002; Reddi et al., 2003; Usher & McClelland, 2001). In the first case, the accumulation can be positive or negative depending on which option the evidence favors while in the second case the accumulation is positive regardless of the option (Audley & Pike, 1965; Van Zandt et al., 2000). Moreover, using two accumulators offers the possibility of choosing whether their accumulation is independent (Brown & Heathcote, 2005; LaBerge, 1962; Logan, 2002; Reddi et al., 2003; Shadlen et al., 1996) or whether it depends on accumulation level of each other via inhibitory connections (Bogacz et al., 2006a; Cisek, 2006; Mordkoff & Yantis, 1991; Usher & McClelland, 2001; Zemliak & MacInnes, 2022). Besides their number, the accumulator(s) can also vary in the way they gather evidence, according to the temporal profile of the integration as well as to the amount of

information integrated at each time interval (sample). Regarding its temporal profile, the accumulation is considered as discrete or continuous over time, depending on whether the time interval used is linearly or exponentially distributed, respectively (Pike, 1973; Ratcliff, 1978). Regarding the amount of information, the integration of evidence at each sample can be “complete” or “partial” depending on the model (Cisek et al., 2009; Cisek & Thura, 2022; Ratcliff, 1978; Usher & McClelland, 2001). The complete integration of evidence is based on the idea that the passage of time ensures the decision accuracy; in other words, the longer the deliberation, the greater the precision. However, a number of studies have shown that after a certain decision duration, the percentage of accuracy reaches an asymptote, saturating the accumulation process (Heitz, 2014; Murphy et al., 2016a; Steinemann et al., 2018; Swensson, 1972; Wickelgren, 1977). While some models attribute this saturation to a noise-related consequence, others use a passive temporal decay to explain this phenomenon (Cisek et al., 2009; Cisek & Thura, 2022; Ratcliff & Rouder, 1998; Usher & McClelland, 2001; Zemliak & MacInnes, 2022). More precisely, the latter implement a leaky integrator with an exponential property representing a partial loss (i.e., a decay) of sensory information at each time interval, leading successive samples to be less informative over time as shown on Figure 1 (Zemliak & MacInnes, 2022). The advantage of such a mechanism is to avoid accumulating redundant information, making the accumulation particularly sensitive to changes in evidence within the environment. Critically, accumulation is not the only mechanism that can differ from one model to another. Indeed, their action selection mechanism can also change. More precisely, some models follow an absolute stopping rule where the action is selected when one option reach a particular amount of evidence (absolute threshold). Others use a relative

stopping rule where the action is selected only if the evidence accumulated for one option exceeds that for the other alternative (relative threshold). While models with just one accumulator always use an absolute threshold (that is actually equivalent to a relative one), those with two accumulators can implement both, a relative threshold (Ratcliff & Smith, 2004; Reddi et al., 2003; Shadlen et al., 1996) or an absolute one (Brown & Heathcote, 2005; Usher & McClelland, 2001; Zemliak & MacInnes, 2022). A last difference that has been widely discussed in the literature concerns the dynamics of the threshold (Hawkins et al., 2015; Hawkins & Heathcote, 2021; Huang & Rao, 2013; Karşılar et al., 2014; Voskuilen et al., 2016; Zhang et al., 2014).Traditionally, the models have considered it as fixed over time (Audley & Pike, 1965; Brown & Heathcote, 2005; LaBerge, 1962; Ratcliff, 1978; Stone, 1960). However, although these models provide a good estimate of decision durations for tasks with a single level of difficulty, they are less effective as soon as tasks include two or more trial types (Cisek et al., 2009; Ditterich, 2006; Drugowitsch et al., 2012; Malhotra et al., 2018). Based on these observations, new models have been developed with an adjustment of the selection threshold over the time course of a trial (Barendregt et al., 2022; Ditterich, 2006; Kilpatrick et al., 2019; Malhotra et al., 2018; Thura et al., 2012). The intuition behind these models is that a dynamic threshold would be optimal for maximizing the rate of reward per time unit, by adapting the behavior to the different types of trials.

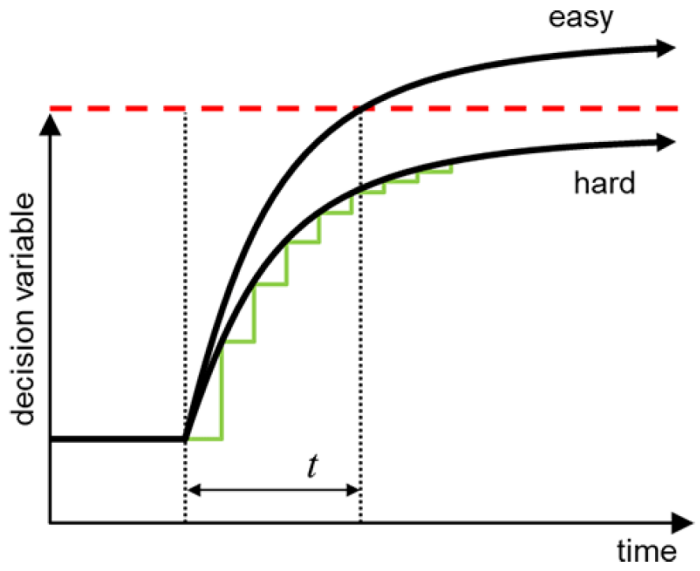

Figure 1. Decreasing rate of build-up in tasks with partially redundant information. Each green step illustrates the novel information contributed by an individual sample. Because this decreases over time, the total accumulated information (black lines) slows down, resembling a low-pass filter or "leaky" integrator. Note that although this may not be a problem for very easy trials, in hard trials the accumulated information may never reach the threshold. Figure and legend from Cisek et Thura (2022) with agreement.

My PhD project focuses on two models. The first one, called "drift diffusion model" or "DDM", is the most widely used in the literature (Berkay et al., 2018; Carsten et al., 2023; Dutilh et al., 2013; Herz et al., 2017, 2018; Lerche & Voss, 2019; Purcell & Kiani, 2016; Rafiei & Rahnev, 2021; Soutschek & Tobler, 2023). In this model, evidence is accumulated at discrete time intervals through one accumulator from a starting point z to a fixed decision threshold T (see Fig. 2). Decision making here depends on three main factors: the amount of evidence required to decide (determined by the distance between the starting point z and the selection threshold T), the speed of evidence accumulation (commonly known as the drift rate) and the noise. Computationally, decision duration may be formalized as follows:

$$\frac{dx_T}{dt} = a \times E_T(t) + c\frac{dW}{dt} \quad (1)$$

Where x_T is the decision variable for the selection probability of choice T over choice $-T$. a represents the drift rate, which is the gain mulipliying the evidence signal for choice T at time t ($E_T(t)$). The last term in the equation implements a white noise process with mean 0 and variance c^2dt.

Interestingly, the "distance to the threshold" is seen as inherent to the subject's decision policy while the drift rate is influenced by multiple factors, such as the level of evidence and the subject's level of arousal (Ratcliff & McKoon, 2008; Ratcliff & Smith, 2004). In order to estimate several decision durations without changing the value of parameters (i.e., drift rate, starting point and selection threshold), a variability across trials is incorporated to specific parameters. Interestingly, such variability also plays a role in differentiating decision durations between correct and incorrect decisions (Bogacz et al., 2010; Forstmann et al., 2016; Rafiei & Rahnev, 2021; Ratcliff, 1978; Ratcliff & Rouder, 1998). More precisely, by adding a variability across trials at the starting point, models can predict shorter decision durations for errors than for correct decisions. Moreover, by adding a variability at the drift rate, they can, in this case, predict longer decision duration for errors than for correct trials. Beside the decision making process, the DDM estimates the duration of two other processes: one responsible for information encoding (i.e., the time required for the nervous system to detect and encode the stimulus) and one responsible for response execution (i.e., the time required for the nervous system to execute the selected action). They are generally lumped in a single **non-decision** parameter (Ter) and added to decision duration (DD), to derive the predicted reaction time (RT): $RT = DD + Ter$ (Myers et al., 2022; Ratcliff & McKoon, 2008). A term

of variability across trials is also incorporated to this last parameter, to estimate the decision duration for extremely fast errors (Forstmann et al., 2016; Rafiei & Rahnev, 2021).

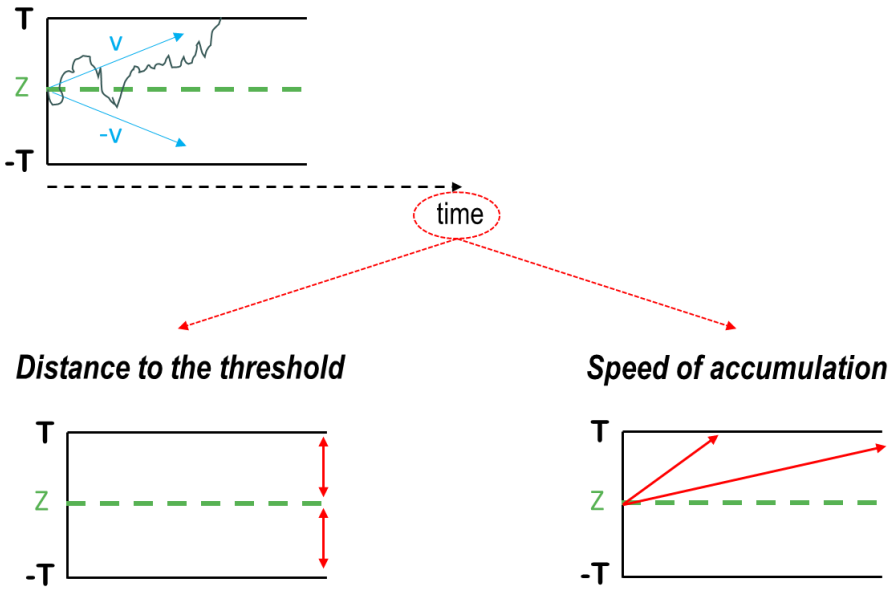

Figure 2. Decision making is a noisy process where decision duration is defined as the time required to accumulate evidence from a starting point (Z, green dotted line) to a selection threshold (T, black lines). The time taken to make a decision depends on three main factors: the amount of evidence required to decide (Distance to the threshold, bottom left), the speed of evidence accumulation (Speed of accumulation, bottom right) and the noise.

Even if the DDM is popular in the literature, it does not appear optimal for all situations. As previously explained, using a fixed threshold constrains the tasks in which decision durations can be effectively estimated (the task with one level of difficulty). This limitation has led to new computational suggestions, including the "urgency gating model" or "UGM", which is the second model I have focused on during my PhD (Carland et al., 2019; Cisek et al., 2009; Cisek & Thura, 2022; Derosiere et al., 2021, 2022; Ferrucci et al.,

2021; Thura et al., 2014). The UGM remains close to the DDM with an accumulation at discrete time intervals through one accumulator, but, it entails three major differences. First, in this model, the integration of evidence is considered as partial, with the computation of a leaky integrator. Secondly, evidence accumulation is influenced by a time-varying gain, called “urgency signal”. Computationally, this signal is typically modelled as increasing linearly over time pushing the starting point close to both selection thresholds, which is mathematically equivalent to a lowering of the latter (Churchland et al., 2008; Cisek et al., 2009; Ditterich, 2006; Murphy et al., 2016a; O’Connell et al., 2018; Thura, 2020). More precisely, the urgency signal includes an intercept, which reflects the degree to which the starting point is upregulated (i.e., the distance to the threshold is decreased) and a slope, which reflects how fast the distance to the threshold will be reduced as time elapses. Note that because urgency signal is computed as a multiplication, it decreases the distance to both thresholds equally. Consequently, it does not introduce a bias towards one action over the other in the decision making process. Such gain was first suggested by Ditterich (2006) to constrain the time wasted in making a decision when the level of evidence is low (i.e., how the threshold is reached when the drift rate is low). Finally, the UGM is restricted to the decision making process and does not include the duration of the non-decision parameter in his computation. Therefore, to compare the decision duration estimated from the model with the real data, one has to estimate the duration of non-decision processes from simple tasks before subtracting it to the RT of the main task, keeping only the decision duration for each trial (Derosiere et al., 2022; Ferrucci et al., 2021; Thura et al., 2014). So, the decision duration is computed here as:

$$\tau \frac{dx_T}{dt} = u(t) \times (E_T(t) - x_T) + c\frac{dW}{dt}, \quad (2)$$
$$u(t) = mt + b$$

Where, as in the equation 1, the variable x_T is the “decision variable” that keeps track of the evidence in favor of choice T. But in the UGM, the equation defines a leaky integrator considering only changes in evidence, which are then multiplied by an urgency signal $u(t)$. This gain is defined as a simple linear function with slope m and intercept b. The last term implements a white noise process with mean 0 and variance c^2dt.

Since the UGM was first developed, it has often been compared with the DDM (Carland et al., 2015, 2016; Cisek & Thura, 2022; Evans et al., 2017; Ferrucci et al., 2021; Winkel et al., 2014). Over the studies, it has appeared that both models, the DDM and UGM, make quite equivalent estimations of decision durations for tasks with a constant level of evidence (Cisek & Thura, 2022). Yet, the UGM typically outperforms the DDM for dynamic tasks where evidence changes over the course of the trial (Ferrucci et al., 2021; Trueblood et al., 2021). Importantly, the aim of my PhD was not to compare these two models, but simply to use them according to the hypotheses and previous results available in the literature, as explained later, in the last section of the global introduction (see summary of objectives).

Past studies of contextual adaptations using DDM and UGM

Several studies have already investigated how human and non-human animal behavior is adapted under time pressure (Arnold et al., 2015; Carsten et al., 2023; Chittka et al., 2009; Derosiere et al., 2022; Heitz, 2014; Herz et al., 2017; Mulder et al., 2013; Ratcliff, 1978; Ratcliff & Rouder, 1998; Spieser et al., 2017; Thura, 2020; Thura et

al., 2014; Vanunu & Ratcliff, 2023; Zhang et al., 2014). Creating such an urgency to respond, they found that subjects shorten their decision duration. At the computational level, this shortening is typically associated with a reduction in the selection threshold in the DDM (Arnold et al., 2015; Carsten et al., 2023; Herz et al., 2017; Mulder et al., 2013; Ratcliff, 1978; Ratcliff & Rouder, 1998; Vanunu & Ratcliff, 2023; Zhang et al., 2014) and with an increased urgency intercept in the UGM (Derosiere et al., 2022; Thura, 2020; Thura et al., 2014). Both of these effects are mathematically equivalent and result in a reduction in the amount of evidence required to select an action. By contrast with the DDM, the slope of the urgency signal in the UGM suggests an increase in urgency with the passage of time, resulting in a gradual decrease in the amount of evidence required to reach threshold, whatever the context (i.e., the initial time pressure). Consistently, decisions following a long deliberation are typically based on a lower level of evidence than decisions made faster (Cisek et al., 2009; Derosiere et al., 2019; Thura et al., 2014). The advantage of a rising signal is that it allows deliberation to start with a relatively “low urgency” (high threshold), to avoid quick errors in easy trials (i.e., with a high drift rate), but then still to end with a relatively “high urgency” (low threshold) to avoid waiting forever in difficult trials with little evidence (i.e., with a low drift rate). Hence, it provides a better ratio between speed and accuracy than DDM using a fixed threshold (Evans et al., 2020). Indeed, in order to ensure rapid decision making in difficult trials under time pressure, a fixed threshold must be greatly reduced from the beginning, leading to some incorrect decisions in easy trials.

Regarding the drift rate, the impact of the urgency context is less consistent in the literature. In most cases, the drift rate remains unchanged under time pressure (Herz et al., 2017; Lerche & Voss,

2019; Mulder et al., 2013; Ratcliff & McKoon, 2008; Vanunu & Ratcliff, 2023; Wagenmakers et al., 2008; Zhang et al., 2014) and is sometimes increased (Arnold et al., 2015; Evans et al., 2020; Rae et al., 2014) or decreased (Carsten et al., 2023; Evans et al., 2020). However, the few effects found had very low statistical power, leading to the conclusion that drift rate is probably not impacted by urgency (Evans et al., 2020). By contrast, the reduction of the distance to threshold is often accompanied by a shortening of non-decision processes (Arnold et al., 2015; Carsten et al., 2023; Lerche & Voss, 2019; Mulder et al., 2013; Vanunu & Ratcliff, 2023; Zhang et al., 2014). The DDM does not dissociate evidence encoding and motor execution, but, behavioral data support, at least, the impact of urgency on motor execution. Indeed, fast decisions are typically followed by faster movements (Carsten et al., 2023; Churchland et al., 2008; Drugowitsch et al., 2012; Thura, 2020; Thura et al., 2014). Interestingly, the reverse relationship has been also reported: two studies have revealed that when the context requires subjects to perform fast movements, the decisions leading to them occur faster, compared to contexts in which subjects have to perform slower movements (Carsten et al., 2023; Kita et al, 2023). These observations suggest a coregulation of decision and movement speed, though this idea has been questioned lately due to the finding that decision and movement speed do not always correlate (Reynaud et al., 2020; Saleri Lunazzi et al., 2021).

Past studies of post-error adjustments using DDM and UGM

As explained above, under time pressure, subjects shorten their decision duration at the expense of accuracy. However, although decision accuracy is reduced, it remains above the chance level (Carsten et al., 2023; Derosiere et al., 2022; Steinhauser & Andersen, 2019). This suggests that, even under time pressure, behavior results

from a speed-accuracy tradeoff. Therefore, making errors leads to an adjustment in the subject's behavior. These adjustments are typically studied in two-choice reaction time tasks by investigating changes in decision speed and accuracy in trials that follow an error, commonly referred to as ‘‘post-error adjustments’’. Using such tasks, subjects typically slow down after an error, a phenomenon called ‘‘*post-error slowing*’’ (PES; Dubravac et al., 2022; Fu et al., 2019; Nigbur & Ullsperger, 2020; Topor et al., 2021). Traditionally, PES is accompanied by an increase in decision accuracy, suggesting an increase in caution in the response strategy (Beatty et al., 2020; Cavanagh et al., 2014; Purcell & Kiani, 2016; Rabbitt & Vyas, 1970; Siegert et al., 2014; Smith & Brewer, 1995; Steinhauser & Andersen, 2019). Computationally, this increase in precaution has been attributed to an adaptive increase in selection threshold to improve performance in the subsequent trial (Dutilh et al., 2012; Fischer et al., 2018; Purcell & Kiani, 2016; Schiffler et al., 2017). However, PES turned out to be occasionally “maladaptive”. As such, sometimes, slowing down does not necessarily lead to an improvement in accuracy; in fact, PES can even come with a decrease in decision accuracy (Ceccarini et al., 2019; Compton et al., 2021; Eben et al., 2020a; Kirschner et al., 2021; Schroder et al., 2020; Smith et al., 2020).This maladaptive PES is often associated with a reduction in attention that can be translated computationally by a reduction in drift rate (Purcell & Kiani, 2016; Wessel, 2018). Hence, while PES has been consistently reported in the literature, its functional role seems to vary according to the situation where it may improve or not accuracy. These discrepancies raise questions about the function of such a slowdown and the factors that can influence it (Damaso et al., 2020; Kirschner et al., 2021; Wessel, 2018). One of the aims of my thesis

was to assess whether the context in which decisions are made (i.e., context with a high or low urgency level) could be one of these factors.

2.2. Tokens task

We are living in a dynamic world where evidence is continuously changing, providing a variety of action opportunities with varying degrees of payoff. In such an environment, animals are free to decide how long to deliberate before selecting and committing to the action they value the most for the current moment. In order to understand the mechanisms involved in decision making, we therefore need a task that approximates the characteristics of a dynamic environment (i.e., one task where evidence can change over the course of a trial, and where subjects can choose when they have to make their decision). The Tokens task developed by the group of Paul Cisek is a perceptual discrimination task corresponding to such characteristics (Cisek et al., 2009; Derosiere et al., 2019, 2021, 2022; Thura & Cisek, 2014). The following section will focus on this task. First, I will describe the basic principles of the Tokens task. Second, I will discuss how this task proved very useful in highlighting the behavior adaptations under urgency context.

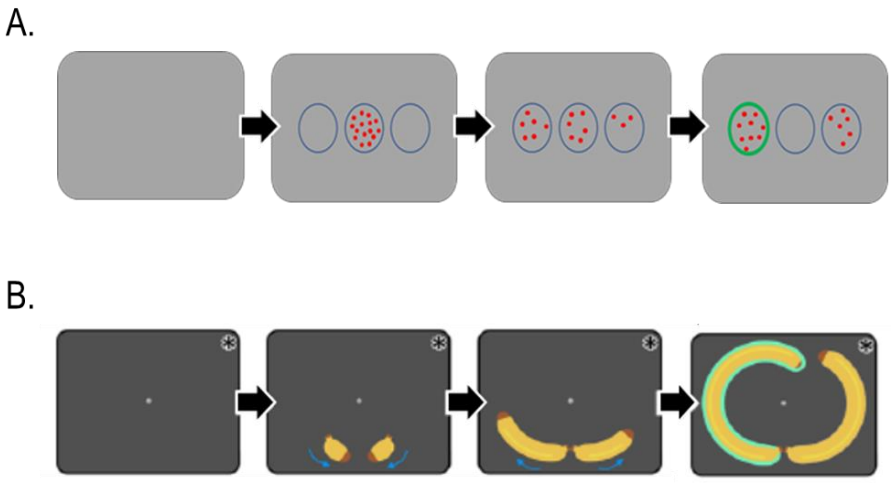

Figure 3. **A. Tokens Task.** Fifteen tokens jumping one by one from a central circle to one of two lateral circles and the subjects have to guess which lateral circle will ultimately receive the majority of the tokens. **B. Banana Task**. Two mini-bananas growing asymmetrically over time by following a circular trace around a fixation point and subjects have to guess which will grow the most.

Basic principles of the Tokens task

Briefly, the Tokens task requires to continuously monitor the distribution of 15 tokens jumping one by one from a central circle to one of two lateral circles (see Fig. 3.A). The subjects are instructed to guess which lateral circle will ultimately receive the majority of the tokens; they have to indicate their choice whenever they want before the last token jump, by performing a movement corresponding to one of the two lateral circles. An adaptation of the Tokens task has recently been developed in our lab (Carsten et al., 2023). In this version, tokens animation is replaced by 2 mini-bananas growing asymmetrically over time by following a circular trace around a fixation point (see Fig. 3.B). In this task, subjects have to observe the bananas grow and to choose which one will grow the most over the course of the trial. As in the initial task, they can indicate their decision at any time before the end of the trial (i.e., before the two bananas together cover 358° around the

fixation point). The aim of this banana task is to recreate the Tokens task without discrete events (token jumps) in order to avoid eye movements and to be potentially used with electroencephalography.

As mentioned earlier, an advantage of the Tokens task is that, when combined with a simple decision making task, it allows to dissociate the decision duration from the duration of non-decision processes (Derosiere et al., 2019; Ferrucci et al., 2021; Thura et al., 2012). Two simplified tasks have been used in the literature. The most common is a simple reaction time (SRT) task (Carsten et al., 2023; Derosiere et al., 2019, 2021, 2022; Leroy et al., 2023; Reynaud et al., 2020; Saleri Lunazzi et al., 2021; Thura, 2020; Thura et al., 2014; Thura & Cisek, 2014). This task has no decision component, since subjects know the response in advance. That is, they can prepare their movement and wait for all tokens to jump into the pre-selected circle at the same time (go signal) to execute it as quickly as possible. With such a design, the SRT task measures the sum of the delay attributable to sensory processing of the go signal display as well as to response initiation and muscle contraction. Another, less frequently used task is a simple choice reaction time (CRT) task in which the choice component was reduced but still present (Cisek et al., 2009; Ferrucci et al., 2021). In this case, the central circle contained either 1 or 15 tokens, which jumped (together) into one of the two circles at the go signal. Subjects had then to select the circle as quickly as possible after the go signal. Keeping a minimal decision component allows the estimation of the time needed to prepare the motor response. Indeed, there is some evidence that even if subjects prepare their movement in advance in both the SRT and the CRT tasks, their level of preparation is lower in the latter (Quoilin et al., 2019).

Contextual adaptations of the behavior in the Tokens task

Since the Tokens task involves a decision and a movement, it allows us to investigate the interactions that may exist between these two levels of control. One of the aims of my thesis was to investigate how the level of urgency affects the interaction between decision making and movement execution. More precisely, we tested the hypothesis that the speed with which we select an action and execute it are, in part, controlled by a common mechanism. To do so, we manipulated, on the one hand, decision speed and investigated the impact of this manipulation on the execution of the ensuing movement. On the other hand, we manipulated the movement indicating the choice in order to observe how changes in movement speed can affect its selection.

The level of urgency can be varied in several ways (see Heitz, 2014 for review). For instance, in human and non-human primates, it has been manipulated by changing the length of the inter-trial interval (Carsten et al., 2023; Cisek et al., 2009; Thura, 2020; Thura et al., 2014) or by manipulating reward and penalty for correct and incorrect decisions, respectively (Derosiere et al., 2019, 2021, 2022). In the first case, hasty decisions are encouraged by considerably accelerating token jumps once subjects have made their decision, shortening the inter-trial interval. Short interval is known to lead subjects to respond faster at the sacrifice of their accuracy in order to maximize the average reward rate (Carsten et al., 2023; Cisek et al., 2009; Heitz, 2014; Simen et al., 2009; Thura, 2020; Thura et al., 2014). That is, by responding faster, they finish the trial earlier and save time to do something else (i.e., to finish the experiment earlier or to complete additional trials, depending on whether the blocks of the task include a fixed number of trials or a fixed duration, respectively). By contrast,

cautious decisions are favored by reducing the post-decision acceleration of the token jumps, which limits the number of decision opportunities. In other words, when the chances of time-saving are low, the best strategy to maximize the reward rate is to ensure decision accuracy (Heitz, 2014). Another way to induce time pressure is by decreasing the reward as a function of reaction time. Indeed, dropping reward over time pushes subjects to respond as fast as possible (Derosiere et al., 2019, 2021, 2022; Swensson & Edwards, 1971). This time pressure can, however, be tempered by increasing the penalty associated with incorrect decisions (Derosiere et al., 2021, 2022).

Whatever the manipulation used in the Tokens task, studies show that subjects decide more quickly when the context emphasizes speed over accuracy (Carsten et al., 2023; Cisek et al., 2009; Derosiere et al., 2022; Thura, 2020; Thura et al., 2014). This haste is accompanied by a decrease in accuracy, supporting the idea that subjects are adapting their speed-accuracy tradeoff. Moreover, the shortening of decision duration is sometimes accompanied by an acceleration of movement speed (Carsten et al., 2023; Thura, 2020; Thura et al., 2014). Moreover, these changes in movement speed between the two contexts (i.e., between the context favoring decision speed and those favoring decision accuracy) correlate with changes in decision speed, suggesting a coregulation between these two levels of control (Carsten et al., 2023). Critically, in both contexts, movement duration seems to shorten after a long deliberation, suggesting that movement speed is also sensitive to the increase in the urgency signal over the course of a trial (Thura, 2020; Thura et al., 2014). Based on these observations, one hypothesis emerged in the literature: the urgency signal could be the mechanism responsible for the coregulation between decision and movement speed (Thura, 2020).

Interestingly, the coregulation hypothesis suggests that the link between decision speed and movement speed is bidirectional. That is, the speed with which subjects perform their movement can influence the speed of the decision from which it derives. The Tokens task allows to test this hypothesis by manipulating the movement required to indicate the decision. The movement involved in the task has varied between the different studies, ranging from a reaching movement (Reynaud et al., 2020; Saleri Lunazzi et al., 2021; Thura, 2020; Thura et al., 2014) to moving the mouse of a computer (Ferrucci et al., 2021), to pressing a button on a keyboard (Derosiere et al., 2019, 2021, 2022), to a tapping movement (Carsten et al., 2023). Depending on the movement used, the speed of its execution can be either directly manipulated by time constraints (i.e., giving a minimum or maximum time to perform it) or indirectly by accuracy constraints (i.e., manipulating the difficulty of the movement to be performed).

Four studies have already investigated the interactions between decision making and movement execution, by looking at the impact of movement constraints on decisions with the Tokens task (Carsten et al., 2023; Leroy et al., 2023; Reynaud et al., 2020; Saleri Lunazzi et al., 2021). In a recent experiment in our lab, manipulating the movement speed altered decision speed in a way that was consistent with the coregulation hypothesis (Carsten et al., 2023). As such, here, context requiring subjects to perform faster movements was associated with faster decisions than context allowing the same movements to be performed slower. It is interesting to note that in the study by Carsten et al. (2023), the time allocated for the deliberation and the movement execution were independent, making coregulation between them unattractive for the reward rate; making faster decisions did not allow to shorten the trial/block duration. This led us to think that coregulation of decision and movement may be a ubiquitous feature

of human behavior, one that occurs by default. Yet, in their recent work, Thura and his team have reported a reversed result with slow decisions in context requiring subjects to perform fast relative to slow movements, reminiscent of a tradeoff rather than a coregulation effect (Saleri Lunazzi et al., 2021). Critically, in this study, subjects had to make a certain number of correct choices to complete the experiment. Hence, in that context, the coregulation between the two levels of control would have reduced the probability of making a correct decision and would have been detrimental to the reward rate. Interestingly, they replicated these results by manipulating the constraints on movement accuracy. In this case, the impact of the accuracy constraint on movement speed is based on the idea that movement execution also responds to a rule of a speed-accuracy tradeoff (Danion et al., 1999; Heitz, 2014; Zhai et al., 2004). In other words, the more difficult the movement, the greater the demand for accuracy (high accuracy), resulting in a reduction in movement speed (low speed). By contrast, the easier a movement is, the faster it can be executed (high speed), as the demand for precision is low (low accuracy). In addition to enabling fast movements, easy movements were associated with slower decision durations, suggesting a slowing down of decision durations with a release of accuracy constraints (Reynaud et al., 2020). However, it only seems to be present if the constraints are imposed per block (block manipulation) and not imposed progressively within a block (trial manipulation, Leroy et al., 2023).

In conclusion, studies that have looked at the interactions between decision and movement speed under urgency context have reported mixed findings. Studies on the impact of decision speed on movement execution have led to the most consistent findings even though some studies have failed to observe an increase of movement

speed with a hastening of decisions. Only one of the four studies looking at the impact of movement speed on the pattern of decision speed has shown a coregulation between the two levels of control (Carsten et al., 2023). Importantly, this coregulation was present even though it did not increase the rate of reward. This suggests a common process between decision making and movement execution occurring by default. The three others studies showed some dissociation between the two levels of control, reminiscent of a tradeoff rather than a coregulation effect (Leroy et al., 2023; Reynaud et al., 2020; Saleri Lunazzi et al., 2021). Hence, these collective findings under temporal pressure (i.e., under high urgency) highlight the existence of one mechanism, called “urgency signal”, that automatically coregulates the decision and movement speed. Nevertheless, the lack of coregulation in some studies leads us to believe that the urgency signal depends on various other distinct mechanisms.

Post-error adjustments of the behavior in the Tokens task

Contrary to the adaptation of behavior to a given context, few studies have looked at the adjustment of behavior following an error in the Tokens task. A first study in monkeys showed that post-error adjustments are influenced by the context and error expectation (Thura et al., 2017). More precisely, monkeys slow down after an error and particularly in a context emphasizing decision speed. They also showed that, whatever the context, PES is greater when the error is unexpected compared to when it is expected. Surprisingly, one monkey showed a shortening of decision duration after an error when the context favored decision accuracy, instead of a slowing down. This post-error speeding has already been observed in the literature and seems related to a sense of frustration at the "loss" of reward (Eben et al., 2020c; Gipson et al., 2012; Verbruggen et al., 2017). A second

study looked at behavioral adjustments in humans. It showed a general slowing down after an error, but only in the absence of strict temporal constraints on movement (Saleri Lunazzi et al., 2023). Indeed, when subjects had to follow particular instructions regarding the duration of their movement, no adjustment was observed after an incorrect decision. Hence, consistent with the literature, trial-to-trial adjustments vary widely from one study to another. This variability is probably due to the fact that these adjustments are complex and influenced by multiple factors (Damaso et al., 2020; Kirschner et al., 2021; Wessel, 2018). Critically, the two studies did not use evidence accumulation models to compute the post-error adjustments of the behavior. This may be due to small effect size or an insufficient number of trials making the computation difficult.

2.3. Summary of objectives

The main objective of my PhD was to investigate the role of urgency on motor behavior. In a first project, I evaluated how urgency influences the interactions between decision making and movement execution. For this project, we used the UGM in order to evaluate the link between the urgency signal and our behavioral data (i.e., with decision and movement speed). In a second project, I assessed whether urgency is one of the factors influencing post-error adjustments. For this second project, the observation of behavioral adjustments was based on a limited number of trials, making the computation impossible. In order to interpret our results from a computational perspective, we relied on existing literature that uses the DDM.

3. Chapter 1 : Task goals shape the relationship between decision and movement speed

Fanny Fievez[1]*, Ignasi Cos[2,3] Thomas Carsten[1], Gerard Derosiere[1,4], Alexandre Zénon[5], Julie Duque[1]

Author affiliations : *[1]Institute of Neuroscience, Université catholique de Louvain, Brussels, Belgium. [2]Facultat de Matemàtiques i Informatica, Universitat de Barcelona, Catalonia, Spain. [3]Serra Hunter Fellow Programme, Catalonia, Spain. [4] Centre de Recherche en Neurosciences de Lyon, France. [5]Institut de Neurosciences Cognitives et Intégratives d'Aquitaine, Bordeaux, France.*

Abtract: The speed at which we move is linked to the speed at which we decide to make these movements. Yet, the principles guiding such relationship remain unclear: while some studies point towards a shared invigoration process boosting decision and movement speed jointly, others rather indicate a tradeoff between both levels of control, with slower movements accompanying faster decisions. Here, we aimed (1) at further investigating the existence of a shared invigoration process linking decision and movement and (2) at testing the hypothesis that such a link is masked when detrimental to the reward rate. To this aim, we tested 62 subjects who performed the Tokens task in two experiments (separate sessions): Experiment 1 evaluated how changing decision speed affects movement speed while Experiment 2 assessed how changing movement speed affects decision speed. In the latter experiment, subjects were either encouraged to favor decision speed (fast decision group) or decision accuracy (slow decision group). Various mixed model analyses revealed a coregulation of decision (urgency) and movement speed in Experiment 1 and in the fast decision group of Experiment 2, but not in the slow decision group despite the fact that these same subjects displayed a coregulation effect in Experiment 1. Altogether, our findings support the idea that coregulation occurs as a default mode but that this form of control is diminished or supplanted by a trade-off relationship, contingent on reward rate maximization. Drawing from these behavioral observations, we propose that multiple processes contribute to shaping the speed of decisions and movements.

3.1. Introduction

Every day of our life, we make decisions to interact with our environment in a goal-directed manner. Several models have been developed to explain how we select actions by describing decision making as a process of noisy accumulation of evidence: during deliberation, sensory evidence is accumulated until the total evidence in favor of one of the potential actions reaches a certain threshold, at which point the decision is made and an action is initiated (Gold & Shadlen, 2007; Hanks et al., 2014; Ratcliff et al., 2016). In the context of motor behavior, such accumulation directly converts into an increase of neural activity in the motor cortex, from a starting point to a consistent decision threshold (Cisek & Thura, 2022; Kelly et al., 2021; Ratcliff & Smith, 2004). In these models, the time taken to select a motor act is a direct function of the speed with which motor activity grows (based on evidence) and of the amount of activity required to reach the threshold, which sets the accuracy criterion.

Decisions can be made even when evidence is low or absent, suggesting that the accuracy criterion can be reduced if necessary. For instance, if we unexpectedly reach a junction when driving a car, we must rapidly decide whether to turn left or right, regardless of readiness and evidence, increasing the risk of an inappropriate choice. Past studies have suggested that this decrease in accuracy criterion can be implemented by an evidence-independent rising “urgency signal” pushing motor activity close to decision threshold, which is mathematically equivalent to a lowering of the latter (Churchland et al., 2008; Cisek et al., 2009; Ditterich, 2006; Murphy et al., 2016a; O’Connell et al., 2018; Thura, 2020). Computationally, this urgency signal is typically modelled as increasing linearly over time (Cisek et al., 2009; Derosiere et al., 2019, 2021, 2022; Kelly et al., 2021); it

includes an intercept, which reflects the degree to which motor activity is upregulated already at the onset of the decision process (i.e., context-sensitive effect), and a slope, which reflects how fast motor activity will be pushed towards the decision threshold as time elapses (i.e., time-sensitive effect).

Reward plays an important role in animal behavior and “reward rate” maximization is a prominent principle in the field of decision making (Lemon, 1991; Shadmehr et al., 2019). More precisely, the reward rate is the sum of all rewards acquired through our actions, minus the costs implied over the total time spent (Carland et al., 2019; Yoon et al., 2018). Critically, the urgency signal described in models of decision making is typically considered as useful for maximizing the reward rate (Carland et al., 2019; Charnov, 1976; Thura et al., 2012). That is, by its context-sensitive effect, the urgency signal can shorten the time invested to obtain the reward. In addition, by its time-sensitive effect, it allows to make decisions without waiting indefinitely, even when there is only little or no evidence.

Several observations in both human and non-human primates indicate that the time one takes to decide impacts the speed of the movement implementing the decision (Churchland et al., 2008; Thura et al., 2014; Drugowitsch et al., 2012). That is, faster decisions are typically followed by quicker movements. Interestingly, the reverse relationship has been observed too: one study in our lab has revealed that when the context requires movements to be performed in a shorter time period, the decisions leading to them arise faster, compared to contexts in which subjects have more time to perform the same movement (Carsten et al., 2023). Altogether, these findings suggest that the urgency signal implemented in decision making models may not solely operate at this restricted level but may shape behavior in a

global manner, coregulating the speed of both decisions and movements (Carsten et al., 2023; Thura, 2020). This “coregulation hypothesis” is consistent with the view that the urgency signal serves to maximize reward rate, as in most situations a speeding up of both decision and movement will shorten the time required to obtain a reward (Shadmehr et al., 2019). Also consistent with this hypothesis is the fact that some studies have reported a time-sensitive effect of decision urgency on movement speed: that is, within a given context, movements that are initiated following a longer deliberation are typically faster than movements associated with earlier decisions, reflecting well the linear increase in urgency over time (Thura et al., 2014; Thura, 2020).

The “coregulation hypothesis” has received systematic support from studies investigating the impact of decision urgency on movement speed (Carsten et al., 2023;Thura et al., 2014; Thura, 2020). By contrast, studies that have addressed this relationship inversely, by looking at the impact of movement speed on the pattern of decision speed, have reported mixed findings (Carsten et al., 2023; Kita et al.,2023; Reynaud et al., 2020; Saleri Lunazzi et al., 2021). As mentioned above, we recently observed changes in decision speed in relation to context-dependent adjustments in movement speed that are consistent with the coregulation hypothesis (Carsten et al., 2023). It is interesting to note that in the latter study, the increase in decision speed when subjects had to perform faster movements occurred even when there was no possibility of saving time by doing so; that is, making faster decisions did not allow to shorten the trial/block duration. This led us to think that coregulation of decision and movement may be a ubiquitous feature of human behavior, one that occurs by default even when not required, arising from a neural organization that has developed because most real-life (urgent) situations require rapid

actions (i.e., including fast decisions and fast movements). Yet, in their recent work, Thura and his team have reported a slowdown of decision speed (rather than a speedup) in contexts requiring subjects to perform faster movements (Reynaud et al., 2020; Saleri Lunazzi et al., 2021), reminiscent of a tradeoff rather than a coregulation effect. Yet importantly, this bunch of work used an experimental design in which subjects knew that a block would only end after a fixed number of correct decisions. Hence, here speeding up decisions was detrimental to the reward rate, as the gain of time on a trial basis would have led to lengthening the experiment, given the decline in accuracy that typically accompanies faster decisions.

Based on these collective findings, it appears that if an urgency mechanism exists in the brain, it must interact with other processes that provide human beings with a flexible control of decision and movement for adaptive behavior according to the task goals, as previously suggested (Saleri Lunazzi et al., 2021) but never tested directly. Here, we addressed this idea in two behavioral experiments on healthy young human participants who performed a variant of the Tokens task in different contexts. Specifically, we tested the prediction that decision and movement durations would be linked by default in this task but that this coregulation would disappear in the same subjects when detrimental in terms of reward rate, as a function of the context in which they perform the task.

3.2. Methods

Participants and ethical statement

A total of 62 healthy human volunteers were recruited for this study, but due to technical issues the data were processed on 56 subjects (30 women, 24.6 ± 3.4 years old). All participants were right-

handed according to the Edinburgh Questionnaire (Oldfield, 1971) and had normal or corrected-to-normal vision. None of them had any neurological disorder or history of psychiatric illness or drug or alcohol abuse; and no one was following any clinical treatment that could have influenced performance. The protocol was approved by the Ethics Committee of the Université catholique de Louvain (UCLouvain), Brussels, Belgium (approval number: 2018/22MAI/219) and adhered to the principles expressed in the Declaration of Helsinki. Participants were financially compensated for their participation and provided written informed consent.

Setup and task

Experiments were conducted in a quiet and dimly lit room. Participants were seated in front of a 21-inches cathode ray tube computer screen, placed at 60 cm from the participant's eyes and used to display stimuli during the task. The display was gamma-corrected, and its refresh rate was set at 75 Hz. Participants' forearms were positioned in a neutral position (i.e., at 0 degree of pronation and supination) on a Canadian board (see Fig.1.A), used to standardize and fix the resting position of the index fingers with elastic bands. Moreover, two lasers (targeting the tip of each index finger) were used to indicate the resting position (i.e., 0 degree of index flexion) and the minimum amplitude of the left or right index finger movement required in the task (i.e., 30 degrees of flexion, see Fig. 1.B and below for more details).

We used a variant of the Tokens task (Cisek et al., 2009;Thura et al., 2014) which has already been exploited in various ways in several past studies of our lab (Derosiere et al., 2019, 2022; Fievez et al., 2022) The current version of the task was implemented with Matlab 2016 (The Mathworks, Natick, Massachusetts, USA) and the Cogent

2000 toolbox (Functional Imaging Laboratory, Laboratory of Neurobiology and Institute of Cognitive Neuroscience at the Welcome Department of Imaging Neuroscience, London, UK).

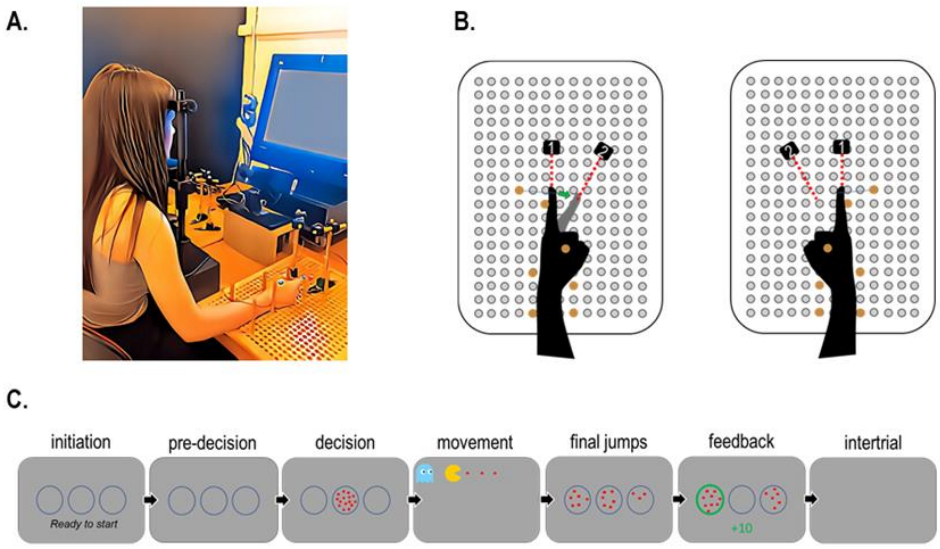

Figure 1. Experimental material A. Setup. Participant forearms were positioned in a neutral position on a Canadian board, with elastic bands maintaining the index fingers in a resting position. **B. Laser device.** Two lasers (targeting the tip of each index finger) were used to indicate the resting position (i.e., 0 degree of flexion; laser 1) and the minimum amplitude (i.e., 30 degrees of flexion; laser 2) of the left or right index finger movement required in the task. **C. Task.** Each trial starts with an initiation phase during which participants have to perform a bilateral flexion of index fingers to signal their readiness. When index fingers return to their resting position, the 3 circles remain empty for a variable pre-decision period (150-300 ms). Then, 15 tokens appear in the central circle and start jumping one by one every 200 ms. Subjects are required to determine, as soon as they feel ready, which lateral circle will end up with the largest number of tokens (left one in this example), and to report their decision with a left or right index finger movement triggering a pacman animation (more details can be found in the main text). Once the movement phase is over, the central circle finishes to empty with the final token jumps. The trial ends with a feedback (fully successful trial in this example; more in the main text) followed by a blank screen of variable intertrial duration (1800-2000 ms).

Sequence of events in a trial

The overall sequence of events for each trial of our task is depicted in Figure 1.C. Each trial starts with the appearance of 3 empty blue circles (4 cm diameter each), placed on a horizontal axis, with the sentence “Ready to start” displayed below them. During this initiation phase, subjects are required to perform a bilateral flexion of index fingers to indicate that they are ready to start the trial. When index fingers return to their resting position, the 3 circles remain empty for a short pre-decision phase of random duration (150-300 ms). The decision phase then starts with the appearance of 15 randomly arranged tokens (0.3 cm diameter) in the central circle that start to jump one by one from the center to one of the 2 lateral circles, every 200 ms. The task of the subjects is to determine which of the two lateral circles will end up with the largest number of tokens and to report their decision with a left or right index finger movement. The movement phase involves a pacman animation that will be described below in more details. Once this phase is over, the final tokens continue to jump until the central circle is empty (i.e., until the 15^{th} token jump; $Jump_{-15}$). Note that subjects are told that they are expected to respond before $Jump_{-15}$, as soon as they feel sufficiently confident. The trial always ends with a feedback (see below for more details) which is followed by a blank screen during a variable intertrial interval (1800-2000 ms).

Trial types and success probability

The difficulty of the decision in each trial of the task depends on the dispersion of tokens along the jumps, which could point more or less obviously to one of the lateral circles. This pattern of token distribution and the degree to which it affects success of the subjects can be formalized with what is called the “success probability”. That is,

for each trial *i*, and at each moment in time, we can define the success probability $p_i(t)$ associated with choosing a response (left or right). If at a moment, the left (L) circle contains *NL* tokens, the right (R) once contains *NR* tokens, and *NC* tokens remain in the central (C) circle, then the probability that the left response is ultimately the correct one (i.e., the success probability of guessing left) is described as follows:

$$p(L \mid NL, NR, NC) = \frac{NC!}{2^{NC}} \sum_{k=0}^{\min(NC,7-NR)} \frac{1}{k!(NC-k)!} \qquad (1)$$

Calculating this quantity for the 15 token jumps allowed us to characterize the temporal profile of success probability $p_i(t)$ for each trial. As such, as far as the participants knew, the individual token jumps and the correct choice were completely random. However, we interspersed distinct trial types within the full sequence of trials. First, in 60% of trials, the $p_i(t)$ remained between 0.33 and 0.66 up to Jump$_{-8}$, that is, the initial token jumps were balanced between the lateral circles, keeping the $p_i(t)$ close to 0.5 until late in these "ambiguous" trials. As such, in ambiguous trials, the tokens jumped alternatively to the correct and incorrect lateral circles until Jump$_{-8}$, such that the number of tokens was equal in both lateral circles after each even jump (i.e., after 2, 4, 6 and 8 jumps) and a difference of one token was present after each odd jump (i.e., after 1,3,5 and 7 jumps). Second, in 20% of trials, the $p_i(t)$ was above 0.7 after Jump$_{-3}$ and above 0.8 after Jump$_{-5}$, that is, the initial jumps consistently favored the correct choice in these "obvious" trials. In the remaining 20% of trials, the $p_i(t)$ was below 0.4 after Jump$_{-3}$, that is, the initial jumps favored the incorrect choice and the following ones favored the correct choice in these "misleading" trials.

Sensory evidence and SumLogLR

As in previous studies (Cisek et al., 2009; Thura et al., 2014; Derosiere et al., 2022), we assumed that participants would estimate the level of evidence based on the number of tokens that have already jumped into the two side circles rather than by calculating the probability of success. This estimation can be computed as a first-order approximation of the real probability function after each jump (see Eq. 1), called the sum of log-likelihood ratios (SumLogLR):

$$SumLogLR(n) = \sum_{j=1}^{n} \log(\frac{p(e_j \mid C)}{p(e_j \mid U)} \quad (2)$$

In this equation, $p(e_j/C)$ is the likelihood of a token event e_j (a token favoring either the chosen or the unchosen response) during trials in which the chosen response C is correct, and $p(e_j/U)$ is the likelihood of e_j during trials in which the unchosen response U is correct. The SumLogLR is proportional to the difference between the number of tokens that favored each of the 2 possible choices (i.e., that moved toward each lateral circle) at any given time.

Index finger movement and pacman animation

As explained in more detail below in the “Experimental design” section, testing our predictions required us to characterize and/or to manipulate the movement features of index finger responses. To allow us to do so, we asked the subjects to provide their response, not with a single finger movement as we usually do, but with a tapping movement involving a repetition of 4 index finger flexions, with the left or right hand depending on their decision in the Tokens task. Moreover, this tapping movement was associated with a pacman animation. That is, as soon as the first tap was completed (i.e., flexion of at least 30 degrees, as indicated by the laser device), a pacman

appeared together with 3 additional tokens in front of it, on a horizontal axis, as shown on Figure 1.C. Subjects knew that each further tap would allow the pacman to “eat” one of these supplementary tokens. The pacman was presented together with a ghost which will be described in the “Experimental Design” section, as its features depended on the experimental condition the subjects were in. Notably, the pacman animation often ended with a blank screen to cover the minimum 3000 ms period of the movement phase: as such, completing the tapping movement faster never allowed to shorten the trial duration, as in Carsten et al, 2023. Finally, note also that trials in which subjects did not provide a response before $Jump_{-15}$ did not involve any pacman animation; in this case participants had instead to remain still in front of a blank screen for a period corresponding to the movement phase duration.

Trial feedback and score calculation

As a feedback at the end of the trial, the chosen circle turned either green or red, depending on whether the choice was correct or incorrect, respectively. The feedback also included a numerical score presented below the central circle, which depended on both the decision and movement requirements of the task. Subjects got +5 points for a correct decision and another +5 points for a correct tapping movement (see below for specific movement requirements). Hence, fully successful trials were worth +10 points (i.e., +5+5), as illustrated on Figure 1.C. Then, any failure, whether at the level of the decision or the movement, was penalized by -2 points. Hence, a partially successful trial was worth +3 points (i.e., +5-2 or -2+5), while a fully failed trial led to -4 points (i.e., -2-2). Finally, in the absence of response before $Jump_{-15}$ (i.e., a no-response trial), the displayed score corresponded to 0 point and came along with a ‘Time Out” message at the bottom of the screen. All trial scores were summed up and

displayed at the end of each block, providing a global feedback on the block to maintain motivation of participants.

Experimental Design

Participants performed two experiments as part of the current study. These experiments occurred on separate days (average interval of 9 ± 8 days) and in a counterbalanced order. In Experiment 1, we designed the task such that, in separate blocks, subjects were either encouraged to make slow or fast decisions. The purpose here was to investigate how these contextual changes in decision speed would influence movement speed. Inversely, in Experiment 2, we aimed at testing the reverse relationship, thus how contextual changes to movement speed (slow or fast) influence decision speed. The specific features of these two experiments are described in the sections below.

Experiment 1

All subjects (n=56) took part in Experiment 1. This experiment required participants to perform the Tokens task in two different block types, where a small adjustment to one trial event (the final jumps phase) allowed us to promote either slow (accurate) or fast decisions (see Fig. 2.A). That is, in the “slow decision” blocks, tokens kept on jumping every 200 ms during the final jump phase, as in the decision phase, until the central circle was empty. In contrast, in the “fast decision” blocks, final tokens jumped much faster (i.e., every 50 ms), such that deciding faster allowed subjects to finish the trial earlier. Because blocks had a fixed duration of 265 sec, deciding earlier in fast decision blocks allowed subjects to perform more trials and thus to accumulate more points. This was not the case in the slow decision blocks, where it was a better strategy to decide later and reach a higher accuracy, given the fixed number of trials (26) that they would

be able to do over the same block duration (always about 265 sec). All of this was made explicit to the subjects to enhance the change in decision policy between the two block types. Finally, as mentioned above, the pacman animation during the movement phase also involved a ghost which, in this experiment, always chased the pacman at a fixed speed established during pilot tests. Subjects knew that they had to avoid the ghost and would get a negative feedback (-2 points, as explained in the feedback section above) if they tapped so slowly that they got caught, in which case the pacman turned into a skull. Yet this happened very rarely because the imposed speed was easy to attain, as it was just there to exhort subjects to do their tapping movement in a row, as opposed to encourage them to go as fast as possible. That is, subjects were able to escape the ghost on most trials, regardless of the block type (see Fig. S1 in supplementary materials).

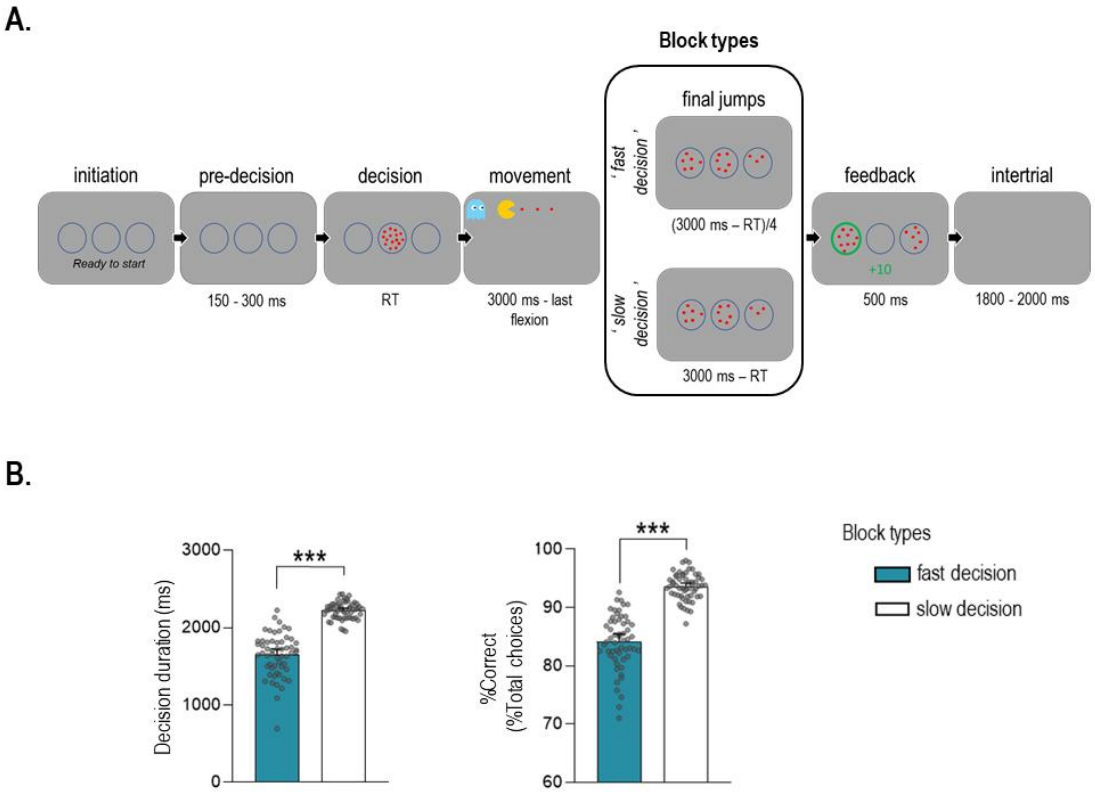

Figure 2. Protocol of Experiment 1. A. Task. In this experiment, participants performed two block types that differed according to the speed at which the final tokens jumped in the lateral circles at the end of the trial (after the finger tapping movement). That is, fast final jumps (every 50 ms) led participants to prioritize decision speed (fast decision blocks) while slow jumps (every 200 ms) led subjects to rather prioritize decision accuracy (slow decision blocks). **B. Manipulation check.** Participants adjusted their decision policy depending on the type of block by making faster (shorter decision duration) and less accurate (lower %Correct) decisions in fast (blue bars) relative to slow (white bars) decision blocks. Error bars represent SE. ***p < 0.001.

Experiment 2

All subjects also performed Experiment 2 but due to a lack of data after cleaning, 2 subjects had to be excluded from the analysis (n=54; 32 Women, 24.5 ± 3.3 years old). As shown on Figure 3.A, in this experiment again there were two different block types, which here differed according to the movement speed requirement. That is, subjects were explicitly asked to report their decision in the Tokens task with a tapping movement that was either fast, in the “fast movement” blocks, or slow, in the “slow movement” blocks. The exact speed that subjects had to adopt in both block types depended on their spontaneous speed. In the fast movement blocks, subjects had to tap at a speed that was twice the spontaneous speed (± 20%), while the speed in the slow movement blocks had to be equal to the spontaneous speed or to any value below it. The spontaneous tapping speed was calculated during a calibration phase at the beginning of the experiment, by asking subjects to perform a block of 15 trials of the Tokens task in a neutral condition, with no specific instruction regarding decision or movement speed. Once the average spontaneous speed was determined based on these trials, the participants were then specifically trained to perform fast tapping movements at the required speed (i.e., twice the spontaneous speed) during 4 blocks for each index finger. In these blocks, subjects repetitively tapped their index finger and each of these movements was followed by a feedback indicating if the tapping was “ok”, “too fast” (>20% above the targeted speed) or “too slow” (<20% below the targeted speed). A block ended as soon as subjects had completed 9 tapping movements at the targeted speed. There was no training for the speed of slow movement blocks as this speed was the one obtained spontaneously.

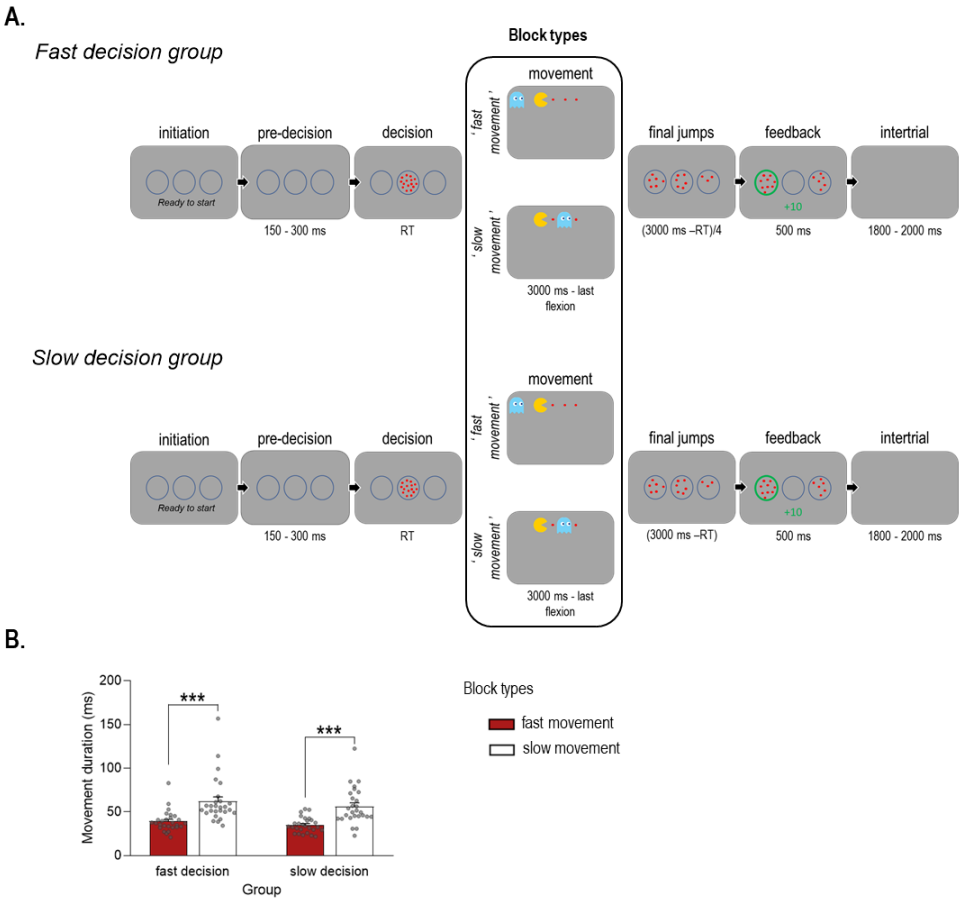

Figure 3. Protocol of Experiment 2. A. Task. In this experiment, participants performed two block types that differed according to the speed at which they had to perform the finger tapping movement; that is, at twice the spontaneous speed (fast movement blocks: pacman chased by ghost) or at about the spontaneous speed (slow movement blocks; pacman preceded by ghost). Moreover, subjects were split into two experimental groups according to whether they performed the version of the task that led them to prioritize decision speed due to fast (every 50 ms) final jumps (fast decision group, upper panel), or to prioritize decision accuracy due to slow (every 200 ms) final jumps (slow decision group, lower panel). **B. Manipulation check.** As required by the instruction in this Experiment, participants displayed shorter (faster) tapping movements in the fast (red bar) than slow (white bar) movement blocks, regardless of whether they belong to the fast or slow decision group. Error bars represent SE. ***$p < 0.001$.

As in Experiment 1, tapping movements in the Tokens task were performed in relation to a pacman (and ghost) animation, where each tap provided the opportunity to “eat” an additional token placed on a horizontal axis. Yet, here the animation served the further purpose to control for the movement speed instruction in each block type. First, to provide a guide to subjects, the ghost here was either moving behind the pacman, chasing it, in the fast movement blocks, while it was preceding the pacman, in the slow movement blocks (see Fig. 3.A). Given the continuous requirement to avoid a collision with the ghost, this feature reminded the subjects to tap rapidly (to escape the ghost) in the fast movement blocks and incited them to tap tranquilly (to avoid bumping into the ghost) in the slow movement blocks.

Importantly, a specificity of Experiment 2 is that we separated subjects in two groups who performed the slow and fast movement blocks in slightly different contexts, due to a small difference in the Tokens task. That is, the final tokens either jumped every 50 ms or every 200 ms, allowing subjects to shorten the trial duration by deciding faster in the group performing the task in the former condition (fast decision group) but not in the group using the latter version (slow decision group). Here, the number of trials was always fixed such that shortening the trial duration never allowed to do more trials. Yet, by responding faster, subjects could save time and finish the experiment earlier. Even if these specificities remained implicit in this experiment, we expected that they would lead subjects to adjust their decision speed such that it would be generally faster in the fast decision group (n=27; 15 women, 25.1 ± 3.6 years old), and generally slower in the slow decision group (n=27; 17 women, 23.9 ± 2.9 years old). With these two groups, we aimed at testing the hypothesis that a default mode of coregulation can be observed when it naturally serves the

reward rate; but it would disappear in situations where it is detrimental to the reward rate. As such, we predicted that tapping faster in the fast movement blocks will translate into faster decisions, compared to the decisions in the slow movement blocks, but that this effect will only be observed in the group of subjects incited to make fast decisions but not in the slow decision group where subjects should better favor decision accuracy. Importantly, each subject completed the short version of the UPPS-P Impulsive Behavior (UPPS) scale (Eben, Billieux, & Verbruggen, 2020). We also evaluated their ability to follow movement instructions in order to make sure that the repartition of participants in the two groups was not creating a bias in our results. The analyses showed no significant difference between the two groups of participants, considering their UPPS scores (see Table S1 in supplementary materials) or their movement performance (see Fig. S2 in supplementary materials).

Time course of the experiments

Experiments 1 and 2 had a largely similar time course. They both started with a familiarization phase during which subjects performed a neutral block of 10 trials to become acquainted with the basic features of the Tokens task. Subjects were then informed about the two types of blocks they would realize in the experiment. This led, after a phase of calibration (in Experiment 2 only to establish the fast tapping speed), to a training phase during which subjects practiced for 4 blocks (2 blocks of each type), each involving 15 trials (or a few more in fast decision blocks of Experiment 1). The actual experiment then started and involved a total of 18 blocks (9 blocks of each type), each involving 26 trials (or a few more in fast decision blocks of Experiment 1). Each block lasted on average 4,36 minutes and a break of 2 to 5 minutes was provided between blocks.

Both experiments then ended with blocks consisting of a choice reaction time (CRT) version of the Tokens task. The task in these blocks (always 40 trials) was the same as in the main experiment: subjects had to respond with a left or right index finger tapping movement according to token jumps but here the 15 tokens jumped all at once in the left or right circle. Experiment 1 entailed 1 CRT block with no restriction on movement speed (i.e., “free” movements), whereas Experiment 2 entailed 1 CRT block for each tapping speed (slow or fast) condition, considering that tapping speed may impact reaction time (RT).

Computational approach

In our work we simulated the decision data by using an implementation of the urgency gating model (UGM; Cisek et al., 2009; Thura et al., 2014), in which evidence is multiplied by a linearly increasing urgency, as follows:

$$x_i(t) = E_i(t) \times [gt + b]^+ < T \quad (3)$$

where $x_i(t)$ represents the activity of motor neurons at time *t* in trial *i*, obtained by multiplying the momentary evidence $E_i(t)$ by an urgency signal. *g* and *b* are the slope and the y-intercept of the urgency signal, and $[\ ]^+$ denotes half-wave rectification (which set all negative values to zero). To estimate the level of evidence accumulation, we used the computation of the SumLogLR (see above, equation 2) that we low-pass filtered for dealing with intra-trial stimulus noise when calculating evidence such as the evidence accumulation. The accumulation of evidence can thus be expressed as follows:

$$\tau \frac{dE_i(t)}{dt} = -E_i(t) + (SumLogLR(t) + N(t)) \quad (4)$$

The Term $N(t)$ represents Gaussian noise with a mean of zero and a SD of 0.7 and, we used a linear differential equation with a time constant τ = 200 ms as low-pass filter (Cisek et al., 2009).

The model has three parameters: *g*, *b* and *T*. To fit the data, we performed an exhaustive parameter grid search, with *g* ranging from 1 x 10^{-7} to 4, *b* from - 1 to 3 and *T* from 1 to 3. This was performed separately for each subject and each block condition, and the quality of fit was assessed by using the mean square-error between data distributions of the model and the real data distributions for all decision times in the interval between 600 and 3000 ms. Importantly, the threshold was not fixed between participants (i.e., ranged from 1 to 3) but was fixed across block conditions (i.e., for fast and slow conditions of the same experiment) to be able to compare the urgency parameters between them. After determining the best fitting parameters for each dataset, we generated a subsequent grid search from the average of the gain and slope of all subjects to determine the best pairs of parameters for a given threshold. This procedure was repeated up to 100 times to ensure parameter optimality convergence, we computed the mean shape (linear function based on g and b parameters) of the resulting urgency functions.

3.3. Data analyses

Behavioral data were collected by means of custom Matlab scripts (MathWorks, Natick, Massachusetts, USA). Statistical analyses were performed using JASP (Wagenmakers et al., 2018b) for repeated-measures analyses of variance ($ANOVA_{RM}$), t-tests and Spearman's correlations, and using the package gamlj in jamovi (ŞAHİN & AYBEK, 2020) for linear mixed models.

Data processing and definition of endpoint measures

In general, trials with poor performance in the decision phase and/or in the movement phase of the Tokens task were excluded in both experiments. This concerned trials with no response before $Jump_{-15}$ or with an anticipated response (before $Jump_{-3}$). This also involved removing trials where the pacman was caught by the ghost and, for Experiment 2, also trials in which the participants did not move at the required speed. Finally, the laser sometimes failed to report the index finger movements and these trials were removed too. As a result, overall, 24% of trials were removed for the analyses (17% for Experiments 1 and 31% for Experiment 2). The same procedure was followed to clean the data in the CRT task, which led to an overall removal of 11% of trials (1% and 20% for Experiments 1 and 2, respectively).

The endpoint measures were the same for Experiment 1 and 2. To characterize the speed at which subjects made their choice, we considered the time they took to decide. This *decision duration* was computed as the average RT in the Tokens task (computed separately for fast and slow blocks with all trial types pooled together) minus the average RT in the corresponding CRT block (Ferrucci et al., 2021). It should be noted that the majority of studies have used the RT in simple reaction time (SRT) tasks to compute the decision duration (Carsten et al., 2023; Derosiere et al., 2022; Thura, 2020), but as we were using different constraints on movement speed, we chose the CRT in order to obtain a measure of the time required to prepare each type of movement (i.e., for free, fast and slow movements). Indeed, there is some evidence that even if subjects prepare their movement in advance in both the SRT and the CRT tasks, their level of preparation is lower in the CRT than in the SRT (Quoilin et al., 2019). Then,

decision accuracy was calculated as the percentage of trials in which subjects choose the correct lateral circle, referred to as *%Correct*. Thanks to the UGM, we also obtained the intercept and the slope of an urgency signal for each participant and each type of block, as an additional primary endpoint measure. These two parameters then enabled us to estimate the evolution of the *urgency level* over time. To characterize the speed at which subjects moved, we considered the time it took for participants to perform the index flexion movements. Hence, *movement duration* corresponds to the mean duration of a single tap averaged over the four flexions participants performed in each trial of the task.

Statistical analyses

Experiment 1

Effect of decision-related instructions on decision endpoint measures

In order to check whether subjects followed instructions and changed their decision policy between fast and slow decision blocks, we first ran paired t-tests on decision duration and decision accuracy. We then considered the urgency signal estimated for each type of block, running a mixed model with BlockType (fast decision, slow decision) as a factor, Time (elapsed during the decision phase) as a covariate and subject number as a cluster variable (*Urgency ~ BlockType * Time + (BlockType * Time|Subject)*). Since we hypothesized a relationship between urgency and decision duration that would hold true across subjects, the covariable was not scaled.

Effect of decision-related instructions on movement endpoint measures

To investigate the context and time-sensitive effect of decision duration, we ran general mixed models on movement duration with BlockType (fast decison, slow decision) as a factor, decision duration as a covariate and subject number as a cluster variable (*Movement duration ~ BlockType * Decision duration* + (*BlockType * Decision duration*|*Subject*)). Our hypothesis was that movement and decision duration correlate within- but not necessarily between-subjects. Hence to get rid of individual average differences in decision duration, we used Z-scores clusterwise to scale the covariable (i.e., decision duration). Post-hoc comparisons were conducted using t-tests with Bonferroni correction for multiple comparisons. Monotonic relationships between block-related changes in movement and block-related changes in urgency/decision were tested using Spearman's rank correlations.

Experiment 2

Effect of movement-related instructions on movement endpoint measures

In order to check whether subjects followed instructions in both groups and changed their movement speed between fast and slow movement blocks, we performed a two-way $ANOVA_{RM}$ on movement duration with BlockType (fast movement, slow movement) as within-subject factor and Group (fast decision group, slow decision group) as between-subject factor.

Effect of movement-related instructions on decision endpoint measures

The analyses for Experiment 2 were similar to those for Experiment 1, except that here, we looked at the reverse relationship by running a general mixed model on decision duration with BlockType (fast movement, slow movement) and Group (fast decision, slow decision) as factors, movement duration as covariable and subject number as a cluster variable (*Decision duration ~ Group * BlockType * Movement duration* + (*Group * BlockType * Movement duration*|*Subject*)).

Exploratory investigation of pupil dilation

In Experiment 1, we recorded pupil diameter from 19 of the 62 participants during task performance. However, one participant did not finish the experiment, so pupil data were analyzed on 18 participants (11 Women, 24.5 ± 3.7 years old). This allowed us to investigate the involvement of the arousal system (proxied by pupil size) in generating the urgency signal (McGinley et al., 2015; Wagenmakers et al., 2018). To this end, the pupil diameter was acquired with an EyeLink 1000+ eye tracker video-based system (SR Research), recording monocularly pupil size (in arbitrary units) and eye movements with a sampling frequency of 1000 Hz. Before analyzing the data, pupil traces were preprocessed to remove eye-blinks, which were identified by the blink detection algorithm implemented in Matlab (https://github.com/alexandre-zenon/pupil/), and replaced by linear interpolations. Furthermore, traces were first filtered by a high-pass filter of 0.01 Hz, then downsampled to 10 Hz to facilitate the analysis. In order to characterize block-related changes in pupil size during the decision phase, we extracted the peak of pupil dilation following the first flexion initiation in each trial (see Fig. S3 in supplementary

materials). We then analyzed these Peak pupil data by means of a mixed model with BlockType (fast decision, slow decision) as a factor, decision duration as covariable and subject number as a cluster variable (*Peak pupil ~ BlockType * Decision duration* + (*BlockType * Decision duration*|*Subject*)). Similarly to the urgency signal analysis, we did not scale the covariable. This analysis allowed us to investigate whether Peak pupil size would evolve as a function of decision duration, as shown for urgency, both in the fast and slow decision blocks. Then, in an additional analysis aimed at further characterizing the evolution of Peak pupil size over time elapsed during deliberation, we obtained for each subject the mean Peak pupil dilation in 8 bins of decision duration (from short to long) and fitted these pupil data with a linear regression to obtain an intercept and a slope. These pupil parameters (intercept and slope) were put in relation to those extracted from the urgency signal (intercept and slope) with Spearman's rank correlations.

3.4. Results

Experiment 1

Subjects adjusted their decision duration according to the block instruction

In this experiment, we had participants perform the Tokens task in fast and slow decision blocks, which required them to favor either decision speed or accuracy, respectively. Consistently, participants took less time to decide in the fast (1647 ± 276 ms) than in the slow decision blocks (2220 ± 111 ms; $t_{1,55} = -15.236$, $p < 0.001$, Cohen's $d = -2.036$, see Fig. 2.B). This shortening in decision duration influenced choice accuracy: participants were less accurate when deciding in the fast decision blocks (84 ± 5 % of correct choices) than in the slow

decision ones (94 ± 2 %; $t_{1,55}$= - 14.175, p < 0.001, Cohen's d = - 1.894). These findings indicate that participants followed the instructions by adopting a strategy favoring speed in the fast decision blocks and accuracy in the slow decision blocks.

Block-related changes in decision duration were reflected in the level of urgency (Thura et al., 2014; Derosiere et al., 2022). Indeed, the mixed model analysis on the urgency signal revealed a main effect of the factor BlockType (see Fig. 4.A, $F_{1,55}$ = 101, p < 0.001): as expected, the level of urgency was on average higher in the fast (0.327 ± 0.166 a.u.) than in the slow decision blocks (0.059 ± 0.107 a.u.). Importantly, this effect was also true when considering the decision period in separate temporal bins (see Table S2 in supplementary materials): the urgency level was higher in the fast than in the slow decision blocks, regardless of the bin considered, up to the last temporal one (all $t_{1,55}$ > 3.760, all p < 0.001, all Cohen's d > 0.500). Moreover, the mixed model analysis revealed a significant effect of the factor Time ($F_{1,55}$ = 112, p < 0.001), indicating that urgency increased as the time elapsed during deliberation in both fast and slow decision blocks, as also previously shown (Cisek et al., 2009; Thura et al., 2014; Derosiere et al., 2022; Murphy et al., 2016; Steinemann et al., 2018). Finally, we observed a significant BlockType x Time interaction ($F_{1,951}$ = 475, p < 0.001), suggesting that the time course of urgency differed between the two block types. To further address this point, we considered the intercept and the slope of the urgency signal (estimated with the urgency gating model) in both block types. Interestingly, paired-t-tests revealed a significantly higher intercept in fast decision blocks (0.195 ± 0.140 a.u.) compared to the slow decision ones (- 0.200 ± 0.251 a.u.; $t_{1,55}$ = 11.097, p < 0.001, Cohen's d = 1.483), indicating a greater urgency at decision onset in the former blocks. However, the urgency exhibited a slower increase in the fast

than in the slow decision blocks. That is, although the slope was significantly positive in both block types (both $t_{1,55} > 5.000$, both $p < 0.001$, both Cohen's $d > 0.700$), it was nevertheless smaller in the fast (0.097 ± 0.125 a.u.) than in the slow decision blocks (0.192 ± 0.119 a.u.; $t_{1,55} = -5.241$, $p < 0.001$, Cohen's $d = -0.700$). Hence, the urgency was generally higher when subjects were in a context promoting fast decisions, with a peak difference at decision onset; from there on urgency increased over time in both block types but did so slower in the fast decision blocks, thus reducing the gap with the slow decision blocks, although the difference remained significant until the end of the decision process.

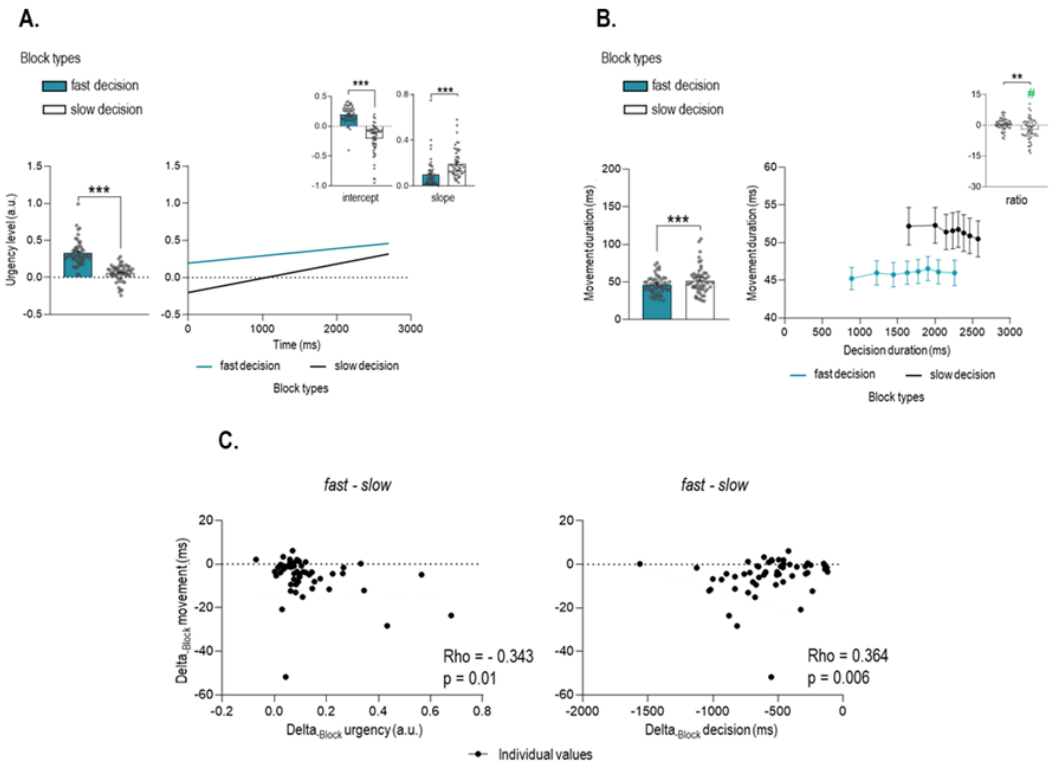

Figure 4. Results for Experiment 1. Results for Experiment 1. A. Urgency signal. The block-related changes in decision duration were reflected in the level of urgency (left panel), with a higher level of urgency in fast (blue bar) than slow decision blocks (white bar). Consistent with the literature, the evolution of the urgency signal over time (right panel) depended on the type of block: it was higher at decision phase onset

(greater intercept, top left inset) and increased more slowly (lower slope, top right inset) in fast compared to the slow decision blocks. **B. Movement duration.** Decisions were implemented by shorter (faster) movements in fast decision compared to slow decision blocks (left panel) even if such a coregulation was not beneficial to the reward rate. Notable, we also found that movement duration shortened with increasing decision duration, but this was only true in slow decision blocks (negative ratio, the inset) **C. Correlations.** The more participants responded with a high level of urgency in fast decision compared to slow decision blocks (higher $Delta_{-Block}$ urgency), the more their movements became shorter (faster) in the fast compared to the slow decision blocks (lower $Delta_{-Block}$ movement; left panel). Similarly, those participants with the largest reduction in decision duration (lower $Delta_{-Block}$ decision) were also those who shortened their movements the most in the fast compared to the slow decision blocks (lower $Delta_{-Block}$ movement; right panel). Error bars represent SE. # t-test against 0 $p < 0.025$. ***$p < 0.001$.

Movement duration was influenced by increasing decision urgency

In this first experiment, we assessed the coregulation hypothesis by investigating the impact of changes in decision urgency on movement duration. Based on this hypothesis and in line with prior work (Carsten et al., 2023; Thura et al., 2014; Thura, 2020), we expected that the higher urgency in the fast decision blocks would also hasten the motor response, resulting in shorter (faster) movements in fast decision blocks. Consistently, the mixed model analysis on movement duration revealed a main effect of the factor BlockType ($F_{1,55.1} = 24.46$, $p < 0.001$), with shorter values in fast (46 ± 12 ms) than in slow decision blocks (51 ± 18 ms, see Fig. 4.B). Moreover, the analysis revealed a significant BlockType x decision duration interaction ($F_{1,47.2} = 11.14$, $p = 0.002$). In order to consider further this interaction, we grouped the movement duration data in 8 bins of decision duration (see Fig. 4.B). Then, we calculated a delta between the mean movement duration of the first and the last bins ($Delta_{-Bin}$) in order to express the change in movement duration across decision duration bins ($Delta_{-Bin}$ movement). The same delta was calculated on

decision duration (Delta$_{\text{-Bin}}$ decision) to finally compute a ratio representing how much movement duration varied as a function of changes in decision duration (i.e., Delta$_{\text{-Bin}}$ movement /Delta$_{\text{-Bin}}$ decision). A negative ratio would indicate a shortening of movement duration with increasing decision duration while a positive ratio would reflect the opposite relationship, that is, a lengthening of movement duration with decision duration. Interestingly, the ratio was negative in the slow decision blocks (- 2.11 ± 5.14; $t_{1,55}$ = - 3.076, $p < 0.025$ with Bonferroni correction, Cohen's d = - 0.411 when compared to 0 using Student's t-tests) but it was null in the fast decision blocks (0.438 ± 2.779; $t_{1,55}$ = 1.180, p = 0.243, Cohen's d = 0.158). Consistently, the ratio was found significantly lower in the slow than in the fast decision blocks (paired $t_{1,55}$ = 3.159, $p < 0.01$, Cohen's d = 0.422). Hence, altogether the analyses indicate globally shorter movement durations in the fast (higher urgency) than in the slow decision blocks but with an acceleration of movement execution over deliberation time occurring in the latter but not in the former decision blocks.

We then continued to investigate the relationship between decision urgency/duration and movement duration by means of correlations. To do so, we computed deltas of movement duration between the fast and slow decision blocks (Delta$_{\text{-Block}}$) and considered the degree to which changes in movement duration between the two block types (Delta$_{\text{-Block}}$ movement) were related to the instructed changes in decision speed. To characterize the latter, we computed both the delta of urgency (Delta$_{\text{-Block}}$ urgency) and the delta of decision duration (Delta$_{\text{-Block}}$ decision), as depicted on the left and right sides of Figure 4.C., respectively. Interestingly, Delta$_{\text{-Block}}$ movement correlated negatively with Delta$_{\text{-Block}}$ urgency (Rho = - 0.343, p = 0.01, 95%-confidence intervals [CI] = [-0.553, - 0.079]), indicating that the more urgency got high in fast compared to slow decision blocks (higher

Delta$_{\text{-Block}}$ urgency values), the more movements became short (fast) in this type of block (lower Delta$_{\text{-Block}}$ movement values). Considering Delta$_{\text{-Block}}$ decision instead of Delta$_{\text{-Block}}$ urgency led to the same result, which here was manifest as a positive correlation (Rho = 0.364, p = 0.006, CI = [0.114, 0.577]): the more subjects shortened their decision duration in fast compared to slow decision blocks (lower Delta$_{\text{-Block}}$ decision values), the more the movements became shorter (lower Delta$_{\text{-Block}}$ movement values). Altogether, these findings are consistent with a coregulation of decision and movement speed (Carsten et al., 2023; Spieser et al., 2017; Thura, 2020).

Experiment 2

Subjects adjusted their movement duration according to the block instruction

In this experiment, we had participants perform the Tokens task in fast and slow movement blocks, which required them to report their decision with either fast or slow index finger flexions. Consistent with these instructions and as shown on Figure 3.B, the ANOVA$_{RM}$ revealed that movements were on average of shorter duration in the fast (37 ± 11 ms) than in the slow movement blocks (59 ± 24 ms; $F_{1,53}$ = 106.879, p < 0.001, partial eta-squared (η_P^2) = 0.673). Moreover, participants in this experiment were split in two groups where they were implicitly encouraged to either favor decision speed (fast decision group) or decision accuracy (slow decision group). Participants in both groups displayed equivalent movement durations according to the specific instructions of the two block types, as indicated by the absence of factor Group or BlockType X Group interaction on movement duration (all $F_{1,53}$ = [0.111, 1.257], p = [0.267, 0.740], η_P^2 = [0.002, 0.024]).

Decision duration was influenced by movement duration

In this experiment, we assessed the coregulation hypothesis by investigating the impact of block-related changes in movement duration on decision urgency. Based on this hypothesis and in line with prior work (Carsten et al., 2023; Kita, et al.,2023.), we expected that the requirement to move fast would naturally increase the urgency, resulting in shorter (faster) decisions in fast than slow movement blocks. Yet, as explained in the introduction, we expected that this should only occur if such a coregulation is not detrimental to the reward rate. In other words, we predicted that moving faster in the fast movement blocks would only translate into faster decisions (higher urgency) in the group favoring decision speed anyway (fast decision group) but not in the group prioritizing decision accuracy (slow decision group).

Unsurprisingly, the mixed model analysis revealed a significant effect of the factor Group on decision duration ($F_{1,55.9}$ = 6.32, p = 0.015). As such, decision durations were shorter in the fast decision group (1997 ± 175 ms) than in the slow decision group (2104 ± 158 ms), as implicitly promoted in this experiment. Furthermore, we found a significant Group x BlockType interaction on decision duration ($F_{1,143.3}$ = 6.82, p = 0.010; see Fig. 5.A). As such, changes in movement duration from the slow to the fast movement blocks elicited distinct effects on decision duration depending on the group. That is, post-hoc analyses revealed that participants in the fast decision group made shorter decisions in fast (1990 ± 183 ms) than slow movement blocks (2004 ± 170 ms; $t_{161.1}$ = 2.957, p < 0.025 with Bonferroni correction). Such an effect was not found in the slow decision group, where decision durations were not significantly different between the fast (2112 ± 164 ms) and slow movement blocks (2096 ± 154 ms; $t_{126.4}$

= - 0.667, p = 1.000). Hence, faster movements led participants to decide faster when such a coregulation was consistent with their task goal, in the fast decision group, but not when it would have been detrimental, in the slow decision group.

The mixed model analysis also revealed a main effect of the factor movement duration on decision duration ($F_{1,16459.4}$ = 8.21, p = 0.004, see right panel of Fig. 5A). Similar to the analysis run in Experiment 1, we grouped decision duration in bins of movement duration (here we used 4 bins) in order to calculate a delta between the first and the last bins on decision ($Delta_{-Bin}$ decision) and movement durations ($Delta_{-Bin}$ movement). These deltas were then used to compute a ratio expressing changes in decision duration as a function of changes in movement duration ($Delta_{-Bin}$ decision/$Delta_{-Bin}$ movement). A Student's t-test against 0 showed that the ratio was significantly negative ($t_{1,53}$ = - 3.152, p < 0.01, Cohen's d = - 0.429) indicating that long movement durations were associated with short decision durations. However, this effect interacted with the factor Group (Movement duration x Group $F_{1,16459.4}$ = 5.00, p < 0.05). More precisely, following Student's t-tests against 0, the ratio was significantly negative in the fast decision group (– 4.606 ± 5.824; $t_{1,26}$ = -4.109, p < 0.001, Cohen's d = - 0.791) but not in the slow decision group (– 0.177 ± 4.392; $t_{1,26}$ = - 0.210, p = 0.835, Cohen's d = - 0.040). This suggests that only in the fast decision group did movement duration vary as a function of deliberation time, as observed in Experiment 1. All other effects of the mixed model were nonsignificant (p = [0.092 0.509]).

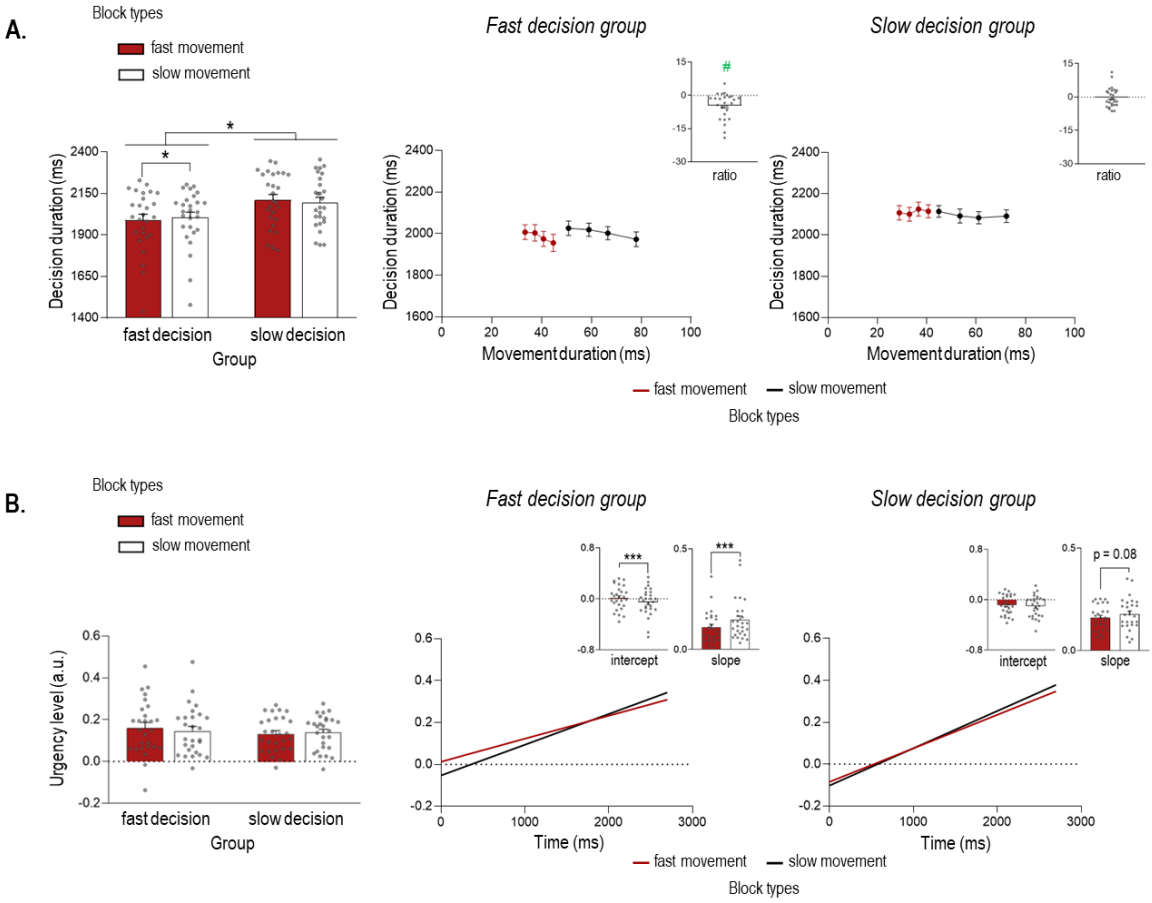

Figure 5. Results for Experiment 2. A. Decision duration. As expected, participants in the fast decision group made faster decisions than those in the slow decision group (left panel). Moreover, as also shown on the left panel, only in the fast decision group were decision durations affected by the movement block type, with shorter (faster) decisions accompanying faster movements (red bar). On the right panel you can also see that long movement durations were associated with short decision durations only in fast decision group (see insets displaying specifically the ratio in the fast and slow decision groups). **B. Urgency signal.** The overall urgency level did not differ significantly between the two groups and the two types of block (left panel). However, as shown on the right panel, its evolution over time differed between the two groups of subjects. More precisely, the movement block type affected the intercept and the slope of the urgency signal in the fast decision group with only a marginal effect on the slope in the slow decision group. Indeed, the urgency signal was higher at the decision phase onset (greater intercept, top left inset) and increased

more slowly (lower slope, top right inset) in fast (red bar) block relative to slow (black bar) movement blocks in the former group only. Error bars represent SE. # t-test against 0 $p < 0.05$, *$p < 0.05$, ***$p < 0.001$.

We then assessed the impact of varying the movement speed in the two different block types on decision urgency itself (see Fig. 5.B). The mixed model analysis revealed a main effect of the factor Time on the urgency signal, consistent with an increasing urgency over time ($F_{1,47.9} = 197.94$, $p < 0.001$). Moreover, we found that this main effect interacted with the factor BlockType, indicating that the urgency signal generally increased faster in slow relative to fast movement blocks (BlockType x Time interaction; $F_{1,916} = 266.65$, $p < 0.001$). Most interestingly, this interaction depended on the Group (Group x BlockType x Time interaction; $F_{1,916} = 32.30$, $p < 0.001$). To better understand this triple interaction, we ran further analyses on the intercept and the slope of the urgency signal (as in Experiment 1). More precisely, paired t-tests revealed a higher urgency intercept in fast (0.013 ± 0.186 a.u.) than slow movement blocks (- 0.053 ± 0.215 a.u.; $t_{1,26} = 2.854$, $p < 0.01$, Cohen's d = 0.549) for the fast decision group, whereas the urgency intercept was around 0.093 ± 0.163 a.u. in both block types for the slow decision group ($t_{1,26} = 0.915$, $p = 0.369$, Cohen's d = 0.176). Hence, urgency was greater at the decision onset in the fast than in the slow movement blocks only for the fast decision group. Yet, it seems that urgency then increased more slowly in fast movement blocks, especially in the fast decision group. Indeed, for this group, the urgency slope was lower in fast (0.110 ± 0.079; $t_{1,26} = -3.645$) than slow movement blocks (0.147 ± 0.103 a.u.; $t_{1,26} = -3.645$, $p = 0.001$, Cohen's d = - 0.701). There was also a trend for urgency slope to differ between fast (0.160 ± 0.061 a.u.) and slow movement blocks (0.178 ± 0.078 a.u.) in the slow decision group, but this

difference was smaller and marginal ($t_{1,26}$ = - 1.83, p = 0.079, Cohen's d = - 0.351). In other words, the urgency signal was higher at the decision phase onset (greater intercept) and increased slower (lower slope) in fast relative to slow movement blocks in the group pushed to decide quickly while it remained mostly unchanged between the two block types in the group pushed to decide slowly. All other effects of the mixed model were nonsignificant (p = [0.154 0.558]). These results suggest that the instruction to boost movement speed in the fast movement blocks induced a parallel increase of urgency when this was consistent with the task goals, in the fast decision group. By contrast, boosting movement speed did not have such an effect in the slow decision group, when it would have been detrimental. In this case, the subjects decided at a similar speed during both slow and fast movement blocks.

We then continued to investigate the relationship between movement duration and decision urgency/duration by means of correlations. To do so, we computed, as in the Experiment 1, the deltas between the fast and slow movement blocks ($Delta_{-Block}$) and looked at how $Delta_{-Block}$ urgency and $Delta_{-Block}$ decision correlated with $Delta_{-Block}$ movement in both decision groups, as depicted on Figure 6. Interestingly, their relationship differed from the Experiment 1. In the fast decision group, there was no relationship with $Delta_{-Block}$ movement whether we considered the $Delta_{-Block}$ urgency (Rho = 0.217, p = 0.276, CI = [- 0.191, 0.538]) or the $Delta_{-Block}$ decision (Rho = - 0.105, p = 0.601, CI = [- 0.451, 0.318]). In the slow decision group, we also found no significant correlation between $Delta_{-Block}$ urgency and $Delta_{-Block}$ movement (Rho = 0.176, p = 0.377, CI = [- 0.213, 0.539]). Surprisingly, we found in this group a relationship between changes in movement duration and decision duration, but here $Delta_{-Block}$ decision correlated negatively with $Delta_{-Block}$ movement (Rho = -

0.510, p = 0.007, CI = [- 0.779, - 0.141]), suggesting that participants with shorter movements in fast relative to slow movement blocks (lower Delta$_{-Block}$ movement values) were those who waited the longest to make their decisions (higher Delta$_{-Block}$ decision values).

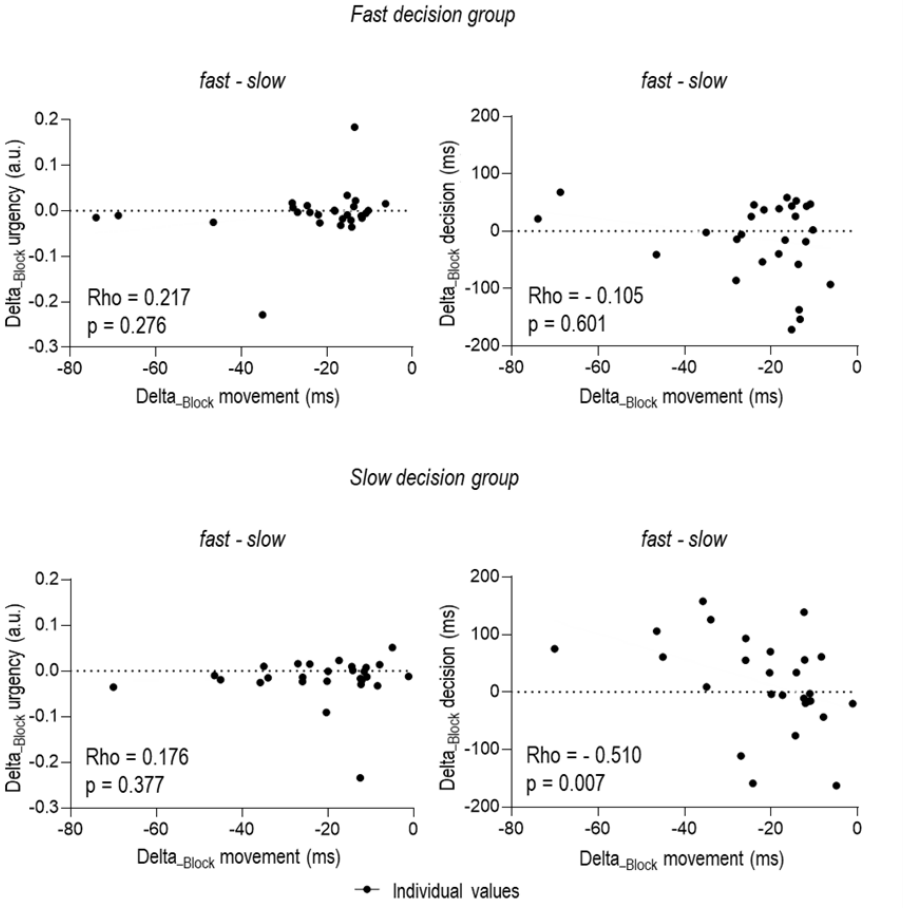

Figure 6. Correlations for Experiment 2. For the fast decision group (upper panel), we did not find any relationship between block-related changes in movement duration (Delta$_{-Block}$ movement) and block-related changes in decision features, whether we considered changes in urgency level (Delta$_{-Block}$ urgency, left) or changes in decision duration (Delta$_{-Block}$ decision, right). For the slow decision group (lower panel), Delta$_{-Block}$ movement did not correlate with Delta$_{-Block}$ urgency (left) but correlated negatively with Delta$_{-Block}$ decision (right).

Note that a significant number of trials were excluded from the analysis because subjects encountered challenges in executing movements at the targeted speed (see related section in Methods for more details). To ensure that this trial exclusion did not mask any potential relationship between decision making and movement execution, we conducted further analyses involving all trials even those in which subjects failed to move as required. This did not change our results, as reported in the supplementary materials (see Fig. S4 in supplementary materials).

In summary, our data in Experiment 2 also indicate a natural coregulation between decision and movement speed when considering the fast decision group in Experiment 2. In contrast, movement speed instructions in the slow decision group did not seem to have any impact on decision speed or on urgency. If anything, the correlations revealed a negative relationship between block-related changes in movement and decision speed in that group favoring accuracy in Experiment 2.

Analyses of pupil dilation

Pupil dilation increased with both urgency and accuracy requirements

Previous studies have shown that increases in urgency induce pupillary dilation (Gross & Dobbins, 2021; Murphy et al., 2016; Reppert et al., 2023; Steinemann et al., 2018). However, the link between pupil dilation and decision urgency is still much debated in the literature. That is, while some have suggested that pupil dilation reflects the involvement of the arousal system in generating the urgency signal (Murphy et al., 2016), others have proposed that the urgency-related pupillary dilation rather results from an increased recruitment of the arousal system to ensure decision accuracy under time pressure

(Steinemann et al., 2018). In order to directly address this question in the current study, we analyzed pupil dilation as a function of decision duration, in 18 of the subjects who took part in Experiment 1.

The mixed model on Peak pupil dilation did not reveal any significant effect of the factor BlockType ($F_{1,8257}$ = 0.616, p = 0.433; 111 ± 57 a.u. for fast decision blocks and 163 ± 74 a.u. for slow decision blocks; see Fig. 7). However, the analysis revealed a main effect of the factor decision duration ($F_{1,8265}$ = 30.173, p < 0.001), indicating that pupil dilation increased with decision duration in both types of blocks. Interestingly, this effect interacted with the factor BlockType (BlockType x decision duration interaction; $F_{1,8265}$ = 30.173, p < 0.001). In order to understand this interaction, we estimated the intercept and slope of the pupil function in each block type by means of linear regressions (see related section in Methods for more details) and compared them across block types. The intercept, which thus reflects pupil size at the onset of the decision phase did not differ between block types ($t_{1,17}$ = 1.049, p = 0.309, Cohen's d = 0.247; 85 ± 71 a.u. and 50 ± 152 a.u. in fast and slow decision blocks). However, the slope (reflecting the speed at which the pupil expanded over decision duration) was steeper in slow (50 ± 152 a.u.) relative to fast decision blocks (5 ± 71; $t_{1,17}$ = - 2.107, p = 0.05, Cohen's d = - 0.497). This result was supported by multiple paired t-tests (Bonferroni corrected) looking at the difference in Peak pupil dilation between fast and slow decision blocks in the 8 bins of decision duration. As such, this additional analysis showed that, in early bins, pupil dilation did not differ significantly between block types but that it became progressively larger in slow than fast decision blocks in the last bins of decision duration (see Table S3 in supplementary materials).

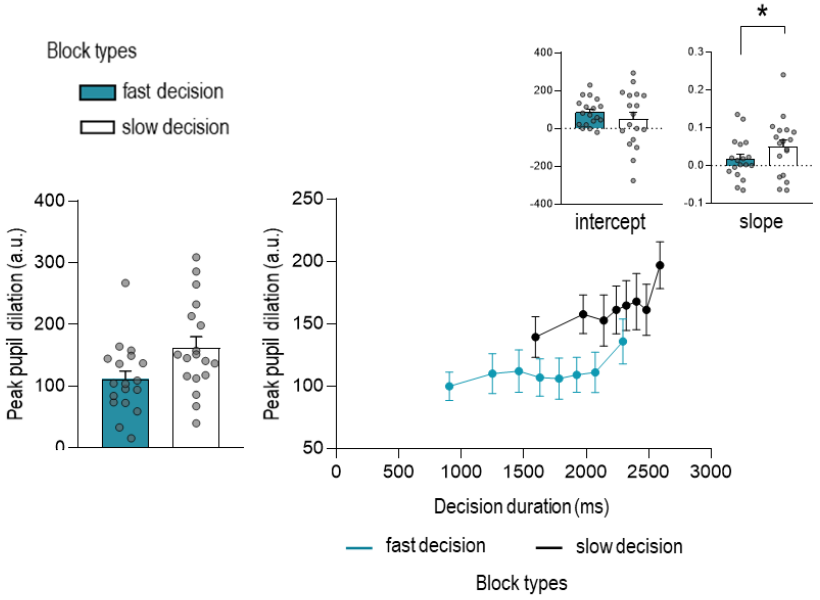

Figure 7. Peak pupil data as a function of decision duration in Experiment 1 (n=18). Peak pupil dilation was comparable in fast (blue bar) and slow (white bar) decision blocks (left panel). Consistent with the literature, Peak pupil dilation increased with decision duration in both types of blocks (right panel). However, while the pupil dilation seemed similar between the two types of block at the beginning of the decision phase (similar pupil intercepts, top left inset), its dilation tended to increase faster in slow decision blocks relative to fast decision ones (higher pupil slope, top right inset), leading to a progressively more dilated pupil in the former. Error bars represent SE. *p < 0.05.

To further investigate the link between pupil dilation and urgency, we put into relation the block-related changes in parameters of both functions. In other words, we looked at how block-related changes in pupil intercept (slope) were linked to block-related changes in urgency intercept (slope). These changes were quantified by obtaining delta values between fast and slow decision blocks (Delta-Block) for the intercept and slope of both the pupil (Delta-Block pupil intercept and Delta-Block pupil slope) and urgency (Delta-Block urgency intercept and Delta-Block urgency slope) functions in all subjects, with thus positive deltas indicating greater values in fast than slow decision blocks. Interestingly, a Spearman correlation on Delta-Block intercept

values revealed a tendency toward a positive correlation (Figure 8; Rho = 0.459, p = 0.057, CI = [0.012, 0.779]), suggesting that participants who showed a greater urgency increase at the onset of decisions in fast than slow decision blocks were also those displaying the larger increase in pupil dilation. Moreover, a positive correlation was found when considering the Delta$_{\text{-Block}}$ slope values (Rho = 0.478, p = 0.047, CI = [- 0.022, 0.803]), indicating that participants whose urgency signal increased more over time in fast relative to slow decision blocks also showed a larger increase in pupil dilation over time.

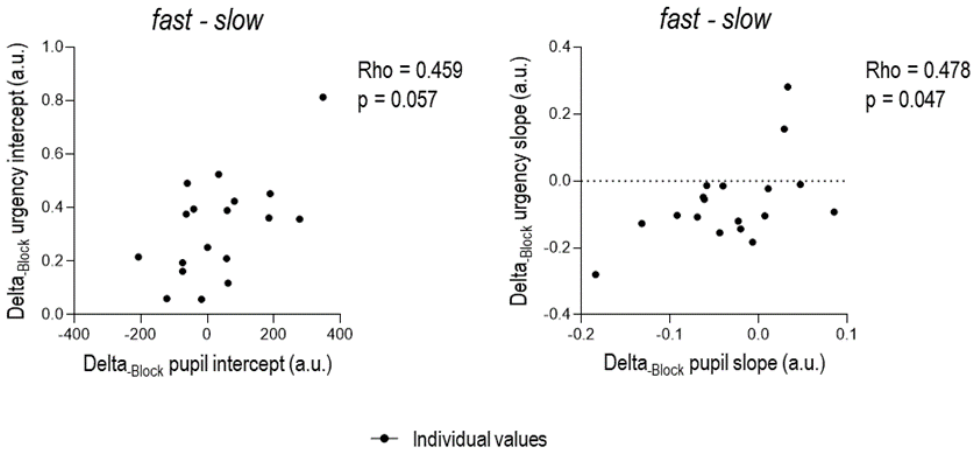

Figure 8. Correlations for Peak pupil data in Experiment 1 (n=18). Block-related changes in the intercept and slope of the Peak Pupil function (Delta$_{\text{-Block}}$ pupil intercept and slope) were related to block-related changes in the same parameters of the urgency function (Delta$_{\text{-Block}}$ urgency intercept and slope). That is, the participants showing a greater increase in pupil intercept (slope) in fast compared to slow decision blocks were also those showing a greater increase in urgency intercept (slope).

Altogether, the effects described above are consistent with a tight relationship between urgency and pupil dilation. Indeed, both urgency and pupil dilation clearly increased with decision duration, and more so in slow decision blocks. Moreover, block-related increases in

urgency intercept and slopes were associated with parallel enlargements in pupil size (though marginal for the intercept). However, we also found that, pupil size tended to be smaller in fast than in slow decision blocks (and significantly so in later bins), contrary to urgency which showed the reverse effect. Such an effect on the Peak pupil data was not related to differences in baseline (tonic) levels of pupil dilation as these values were equivalent in both block types (see Fig. S5 in supplementary materials). Nor was this effect due to the fact that decision durations differed across block types within the same bins (see Fig. 7). Indeed, when considering only a set of equivalent ambiguous trials with long decision durations (i.e., decisions falling between $Jump_{-9}$ and $Jump_{-10}$) and a constant level of evidence (i.e., with a success of probability at decision time equal to 0.8125 in all trials), we found that pupil dilation remained greater in slow decision blocks, although the difference with fast decision blocks was marginal (137 ± 70 a.u. and 105 ± 54 a.u., respectively; $t_{1,15} = 1.97$, $p = 0.067$, Cohen's $d = 0.493$; 2 subjects had to be excluded from this analysis, because of a lack of data).

We then considered the possibility that the larger pupil size observed in slow decision blocks was due to a special focus on accuracy in this condition. As such, subjects had a fixed number of trials here (contrary to fast decision blocks) and they then plausibly recruited all available resource's to be as accurate as possible, including increased arousal. To test this hypothesis, we considered again the subgroup of ambiguous trials described above for which we computed a block-related delta (fast-slow) for the accuracy and pupil data. Interestingly, in those particular trials, the $Delta_{-Block}$ pupil size was positively correlated with the $Delta_{-Block}$ accuracy (Rho = 0.758, $p < 0.001$, CI = [0.501, 0.873]). In other words, the more the pupil was dilated in the slow decision blocks compared to the fast decision blocks

(i.e., the more the Delta$_{\text{-Block}}$ pupil was negative), the more subjects exhibited better accuracy in the slow than in the fast blocks (i.e., the more the Delta$_{\text{-Block}}$ accuracy was negative). In conclusion, variations in pupil-related arousal in the current study seemed to be driven by two overlapping factors: the level of urgency, as expected, and the strategic allocation of resources to promote accuracy.

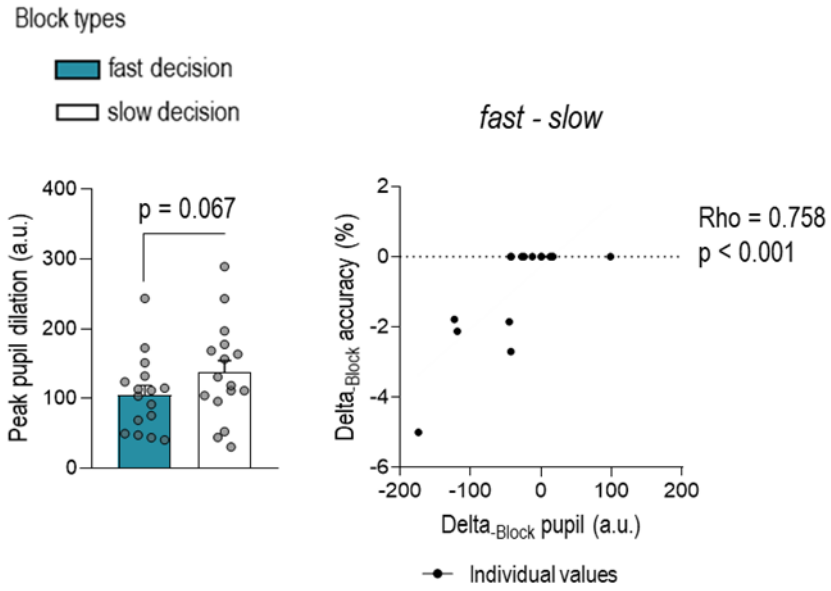

Figure 9. Peak pupil data in ambiguous trials of Experiment 1 (n=16). Peak pupil dilation tended to be larger in slow decision blocks (white bar) than in fast decision blocks (blue bar). Given that deltas were computed by measuring the difference in Peak pupil dilation between fast and slow conditions, the more the subjects showed a greater Peak pupil in slow decision blocks, the more they displayed a negative delta**.** Interestingly, we found that the greater this pupil enlargement in slow compared to fast decision blocks (i.e., greater negative Delta$_{\text{-Block}}$ pupil), the greater the gain in accuracy in slow compared to fast decision blocks (i.e., greater negative Delta$_{\text{-Block}}$ accuracy).

3.5. Discussion

The aim of our study was to provide a principled explanation to the relation between decision and movement speed. Consistent with this, our data supports the hypothesis that coregulation operates as a default mode. However, our findings also show that this form of control can fade or even be replaced by a tradeoff relationship, depending on the task goals. Based on these behavioral observations, we propose that several processes come into play to shape the speed of our decisions and movements either selectively or jointly, the latter mode being best observed when a default coregulation of decision and movement allows to maximize the reward rate, or at least, when it is not detrimental to it.

The relationship between decision and movement speed adapts to context-dependent task goals

Context-dependent changes in decision speed, as elicited in Experiment 1, led to clear changes in movement speed that are consistent with a coregulation of both levels of control. Indeed, subjects made faster movements in fast decision blocks than in slow decision blocks, and these changes in movement speed were correlated with the strength of changes in decision speed: the more subjects adjusted their decision speed according to the instruction, the more they showed a parallel change in movement speed. Note that, similar to Carsten et al (2023), changes in movement speed accompanied block-related variations in decision speed despite its absence of impact on the reward rate, substantiating the view that such coregulation type of control occurs naturally.

Context-dependent changes in movement speed, as required in Experiment 2, also affected decision speed. Yet, the direction of the

effect differed according to the group that was considered. That is, the group whose reward rate was maximized by a strategy favoring decision speed (i.e., the fast decision group) showed faster decisions in fast movement compared to slow movement blocks. Even if this coregulation effect was not as strong as in Experiment 1, it was still significant, pointing to a similar form of coregulation. In contrast, the group whose reward rate was maximized by a strategy favoring decision accuracy (i.e., the slow decision group) did not show such a covariation of decision speed between the slow and fast movement blocks. Quite the contrary, in this group we even observed the reverse relationship. More precisely, although decision speed was similar between fast and slow movement blocks, the changes in movement speed correlated negatively with changes in decisions speed: the more subjects accelerated their movement speed in fast compared to slow movement blocks, the more they slowed down their decision. This is consistent with a tradeoff type of relationship in this (slow decision) group, contrasting with the coregulation effect observed in the other (fast decision) group, despite the fact that subjects from both groups displayed a coregulation effect when manipulating decision speed in Experiment 1.

Interestingly, similar observations regarding context-dependent variations in Experiments 1 and 2 were made when considering directly the relationship between movement speed and decision urgency itself (and not only decision speed), as done for the first time in this study. As such, in Experiment 1, the decision urgency was clearly higher in fast decision blocks compared to slow decision blocks and this upregulation was found to significantly correlate with the changes in movement speed that occurred between the two contexts: the greater the context-dependent increase in urgency level, the more subjects accelerated their movement speed from one block type to the

other. Similarly, the coregulation observed in the fast decision group of Experiment 2 was also apparent when considering the urgency: fast movement blocks were associated with a higher urgency intercept than slow movement blocks in this group of individuals. Such a relationship was not found when the other (slow decision) group was considered. Hence, altogether, these findings indicate that the relationship between decision speed/urgency and movement speed can shift from a coregulation to a tradeoff according to the task goals, which provides an explanation for the apparent discrepancy between findings of past studies (Carsten et al., 2023; Kita et al.,2023.; Reynaud et al., 2020; Saleri Lunazzi et al., 2021).

The deliberation time impacts on movement speed

In our experiment, the level of urgency did not only vary in a context-dependent manner (i.e., between blocks) but also in a time-dependent manner (i.e., over the course of a trial). That is, as shown in many past studies, urgency increased during a trial, pushing the subjects to respond as the trial comes to an end. Consistent with a natural coregulation of decision speed and movement, we observed a time-dependent speeding up of movements over the course of a trial, as already reported in past studies (Thura et al., 2014; Thura, 2020; Thura et al., 2012). Interestingly, this was generally true, whether considering results from Experiment 1 or Experiment 2: overall, movement speed increased as deliberation time (and thus urgency) increased, in a given context.

Yet, an intriguing finding here, is that in Experiment 1, this effect was only observed in the slow decision blocks (generally associated with slow movements) but not in the fast decision blocks (where movements were generally faster due to the context-dependent change in urgency elicited by the task instruction to decide fast). A

possible explanation for this is that the slope of the urgency function was smaller in the fast than slow decision blocks of this experiment, as shown in the past. That is, when subjects put the emphasis on decision speed, the intercept is higher but then the urgency increases more slowly as evident by a smaller slope in fast decision blocks (Thura et al., 2014; Thura, 2020). Hence, the weaker increase in urgency over the course of the trial in the latter block type may be responsible for the absence of time-dependent effect on movement speed in that condition, compared to the slow decision blocks where the slope is steeper following a lower intercept. Nevertheless, previous studies have shown an acceleration of movements with the passage of time, irrespective of the slope size of the urgency signal (Thura et al., 2014; Thura, 2020). Another plausible explanation is that the impact of urgency on movement speed is counteracted by a process controlling the energy cost. More precisely, the energy expenditure as a function of movement duration is represented by a concave upward function for many types of movement (Shadmehr et al., 2016; Steudel-Numbers & Wall-Scheffler, 2009; Yoon et al., 2018; Zarrugh et al., 1974). As the speed of movement is slower in the slow decision blocks than in the fast decision blocks, it is possible that accelerating the movement speed decreases energy expenditure in the former and increases it in the latter. Increasing the energetic cost of movement in the fast decision blocks would lead to a decrease in the value of the reward, and thus the rate of reward. Therefore, limiting the impact of the urgency signal depending on the energy cost seems entirely credible. The fact that previous studies did not observe a ceiling effect for the urgency signal could be linked to the type of movement involved in the task. Indeed, in these studies, the task involved reaching movements, whereas our experiment required index finger tapping movements. Unlike the latter, reaching movements are large and

involve several joints (at least the three articulations of the arm). It is likely that such multi-joint movements offer a wider range of movement speeds than single-joint (tapping) movements.

Pupil dilation reflects an increase in arousal related to urgency and decision accuracy

Converse to previous studies (Gross & Dobbins, 2021; Murphy et al., 2016; Steinemann et al., 2018), the pupil dilation did not differ significantly between fast and slow decision blocks. However, we found an increase in dilation as a function of decision duration, suggesting that pupil dilation may be partly linked to the urgency signal (Gross & Dobbins, 2021; Lawlor et al., 2023; Murphy et al., 2011, 2016; Steinemann et al., 2018). This idea is supported by the similarity found between pupil dilation and urgency signal as well as the positive correlations that were found between their parameters (see Fig. S6 in supplementary materials). Yet surprisingly, unlike the urgency signal, pupil size tended to be more dilated in slow compared to fast decision blocks. Contrasting with previous studies (Gross & Dobbins, 2021; Murphy et al., 2016; Steinemann et al., 2018), this result suggests a recruitment of the arousal system as a function of both urgency and accuracy. One possible explanation is that the emphasis on decision accuracy in slow decision blocks was particularly high in our design. This pressure could arise from the fact that using a fixed number of trials limits the possibility of increasing the rate of reward, giving importance to each trial. The positive correlation between pupil dilation and performance in ambiguous trials supports this idea, showing that the more the pupil was dilated in slow decision blocks, the more subjects increased their accuracy in this condition for a same level of evidence.

Altogether, these results suggest that pupil dilation reflects two overlapping actions. More precisely, the recruitment of the arousal system would, on the one side, increase the gain of sensory information at the decision level with the increase in urgency in the fast decision blocks, and on the other side, increase the attention to enhance accuracy in a context where it is prioritized regardless of urgency, as in our slow decision blocks. The mechanisms through which the arousal system can enhance performance accuracy are still unclear, but may involve enhancing processing of sensory information (Zénon, 2019). This hypothesis is in line with a report by Steinemann and his colleagues, who showed that pupil dilation is associated with better encoding of sensory evidence in the visual cortex. Nevertheless, further studies are needed to investigate the involvement of the arousal system in decision making using causal approaches, using for example techniques such as transcutaneous vagus nerve stimulation (Hilz, 2022).

Several neural mechanisms are likely to shape the relationship between decision and movement speed

Plausible neural source underlying the natural coregulation of decision speed and movement speed

A possible candidate for the coregulation effects observed in our two experiments is the basal ganglia (Chen & Yang, 2021; Dudman & Krakauer, 2016; Kaduk et al., 2023; Desmurget & Turner, 2010). As such, this structure could be at the source of a signal invigorating behavior as a whole to maximize reward rate, as hypothesized in several studies of the last decade (Carsten et al., 2023; Cisek & Thura, 2022; Thura, 2020; Thura et al., 2022; Thura & Cisek, 2017). Reward-sensitivity of the dopaminergic system has been extensively studied in the past (Berridge & Robinson, 2016; Salamone

& Correa, 2024; Schultz et al., 2017; Weinstein, 2023) Consistently, dopamine seems strongly implicated in the control of decision speed and movement vigor (Bourgeois et al., 2016; Coddington & Dudman, 2019; Niv, 2007; Pietro Mazzoni et al., 2007). Interestingly, it is believed that it amplifies motor gain (Park et al., 2020; Yttri & Dudman, 2018), which seems to rely, at least in part, on inhibitory influences increasing the signal-to-noise ratio in motor neural activity (Duque et al., 2017; Greenhouse, 2022; Vassiliadis et al., 2020; Wilhelm et al., 2022). This dopamine-mediated invigoration may be thus responsible for the increased surround inhibition, a phenomenon observed in studies applying transcranial magnetic stimulation (TMS) during movement preparation, which has traditionally been associated with an increase in movement vigor (Dudman & Krakauer, 2016; Shadmehr et al., 2019) but which has also recently been linked to an increase in decision urgency (Derosiere et al., 2022).

Plausible neural source underlying the occurrence of a tradeoff between decision urgency and movement speed

The context-dependent modulations of decision speed as a function of the movement blocks in the slow decision group of Experiment 2 reflects a tradeoff rather than a coregulation of decision and movement speed, despite the fact that there is evidence for a coregulation in this same group in Experiment 1 (see Fig. S7 in supplementary materials). This suggests that the requirement to focus on decision accuracy led this group of subjects to recruit processes allowing to maintain the appropriate level of accuracy despite the fact that switching from slow to fast movement blocks let to a joint invigoration of decision with movement speed. Such hypothesis is supported by a marginal negative correlation found between the UPPS score for urgency and the $Delta_{\text{-Block}}$ of decision duration in the slow

decision group (see Fig. S.8 in supplementary materials). Although non-significant (p-tendency of 0.083), this correlation leads us to formulate a hypothesis for future studies; the more impulsive the subjects are (higher UPPS urgency score), the less they are able to slow down their decisions in fast movement blocks (lower $Delta_{Block\ decision}$). In other words, this suggests a lower ability to counteract the effect of common invigoration, an interesting idea for future investigations. Therefore, it is plausible that a cognitive control process (less efficient in impulsive individuals) can come into play and selectively shape decision parameters in a goal-directed manner, helping to “hold your horses”. This type of inhibitory control mechanism has been widely studied during conflict resolution and during action stopping as an extreme case of braking (Frank et al., 2007; Mosher et al., 2021). Several lines of evidence indicate that it relies on the hyperdirect pathway from medial frontal cortex to subthalamic nucleus (Cavanagh et al., 2011; Forstmann et al., 2008; Herz et al., 2017), producing broad, non-specific inhibition in motor areas to slow down the action selection process (Aron et al., 2016; Duque et al., 2016; Klein et al., 2014; Wessel & Aron, 2017). This effect would be associated with a broad motor cortex suppression as already observed in past TMS studies, showing for instance reduced excitability in leg muscles during cautious finger responses (Derosiere et al., 2022; Duque et al., 2017).

3.6. Conclusion

In conclusion, the interaction between decision and movement speed seems influenced by different mechanisms. Our findings highlight two of them; a common invigoration mechanism responsible for a natural coregulation between decision and movement speed, and a cognitive mechanism, which slows down decisions when the reward

is linked to the precision of the choices. Contrary to expectations, although the urgency signal was influenced by changes in movement speed, it did not always correlate with it, suggesting that this signal reflects a combination of the different mechanisms involved in decision making and not just that of invigoration. Interestingly, our results support a link between pupil dilation and decision urgency, but here also with the additional influence of an accuracy-promoting factor.

3.7. Supplementary materials

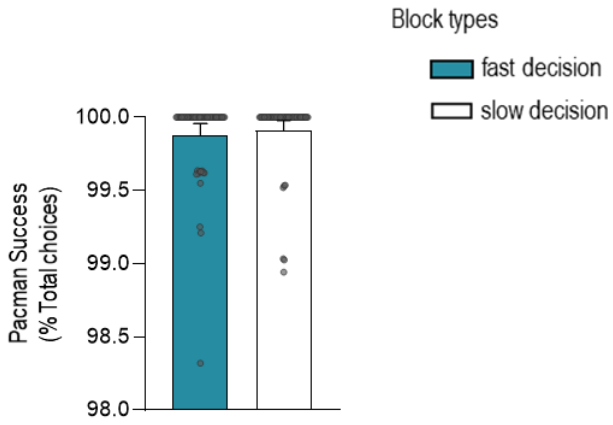

Figure S1. Movement performance in Experiment 1. In order to exhort subjects to do their tapping movement in a row, we added a pacman animation with a chasing ghost during the movement phase (see related section in Methods for more details). Participants successfully escaped the ghost (Pacman Success) equally in fast decision blocks (blue bar) and slow decision blocks (white bar). Error bars represent SE.

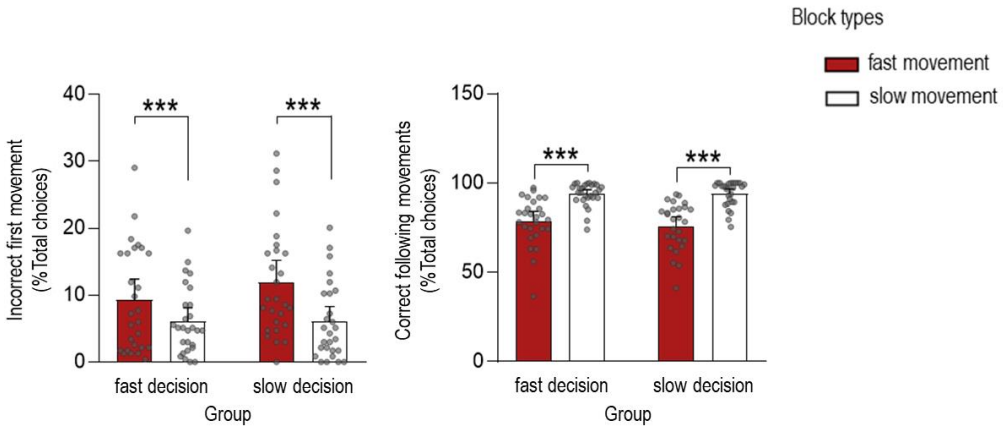

Figure S2. Movement performance in Experiment 2. On average, participants had more difficulty keeping up with the speed imposed in the fast movement blocks (red bars) than in the slow movement blocks (white bars). More precisely, the success rate was lower in fast relative to slow movement blocks for both the first tapping movement (higher percentage [%] of incorrect first movement, left panel) and the following ones

in the movement phase (lower % of correct following movements, right panel). Error bars represent SE. ***p < 0.001.

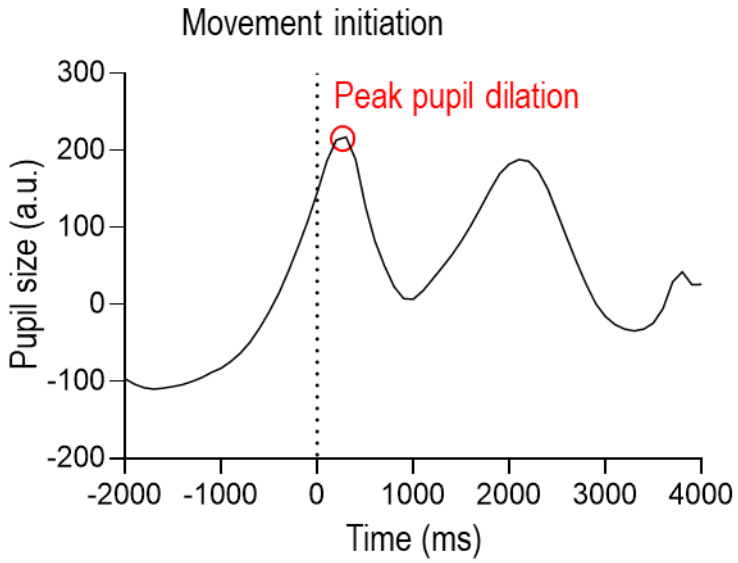

Figure S3. Typical pupil dilation signal. In order to characterize block-related changes in pupil size during the decision phase, we extracted the peak of pupil dilation (Peak pupil dilation) following the first flexion initiation (Movement initiation) in each trial. This figure shows the evoked pupil dilation aligned to movement initiation (0) in one subject.

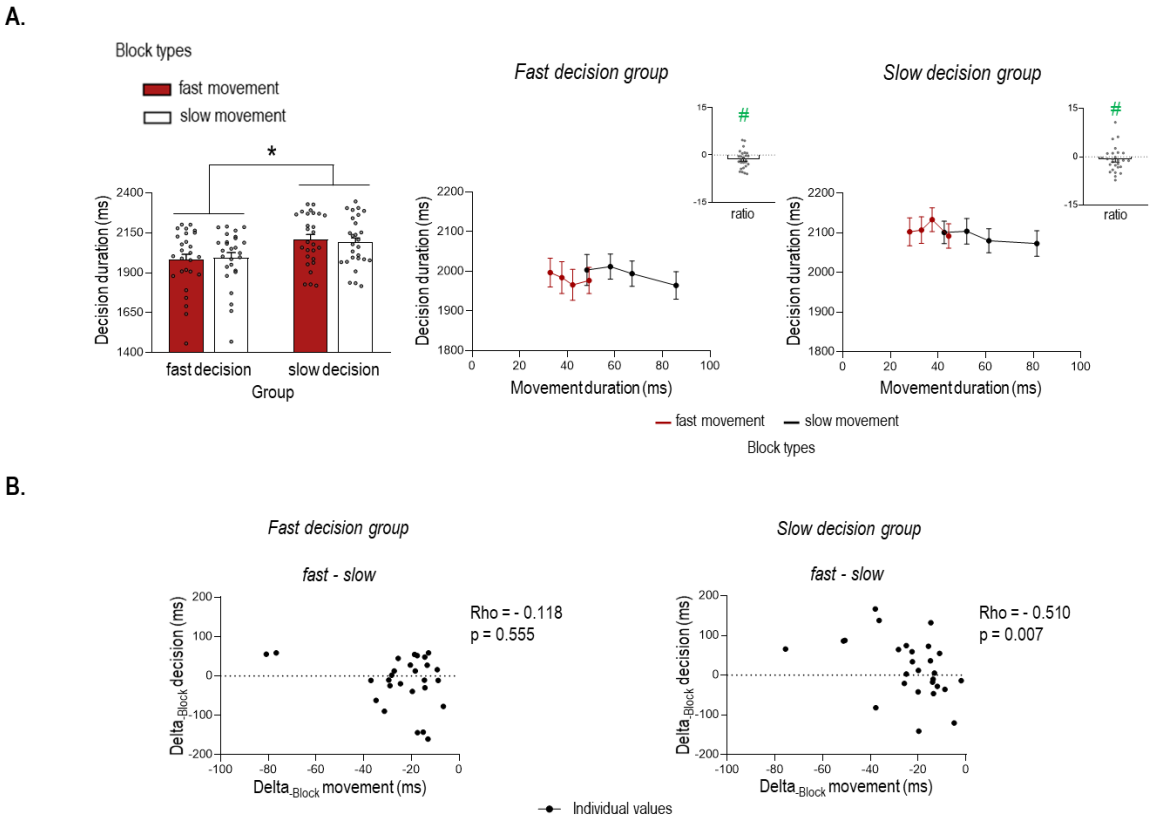

Figure S4. Impact of movement duration on decision duration when including trials in which subjects failed to move as required in Experiment 2. To ensure that the important trial exclusion did not mask any potential relationship between decision making and movement execution, we conducted further analyses involving all trials even those in which subjects failed to move as required. This analysis adopted a more lenient criterion, wherein only trials where subjects completed the Pacman animation with three times as many movements as expected were excluded (overall only 14% of trials were removed for the analysis). **A**: participants in the fast decision group made constantly faster decisions than those in the slow decision group (left panel). Due to the increase in variability, the Group x Block type interaction was not significant anymore ($p = 0.113$). But, this interaction became closer to significance when the analysis was focused on the speed of the first flexion rather than the average speed of all movements ($p = 0.064$). Moreover, long movement durations were associated with short decision durations in both, fast and slow decision groups (right panel; see also insets displaying specifically the decision/movement ratio in the fast and slow decision groups). **B**: we did not find any relationship between block-related changes in movement duration ($Delta_{-Block}$ movement) and block-related changes in decision duration ($Delta_{-Block}$ decision) for the fast decision group (left panel). For the

slow decision group (right panel), Delta$_{\text{-Block}}$ movement correlated negatively with Delta$_{\text{-Block}}$ decision, similar to the analysis reported in the main text on a restricted number of trials. Error bars represent SE. # t-test against 0 p < 0.05, *p < 0.05.

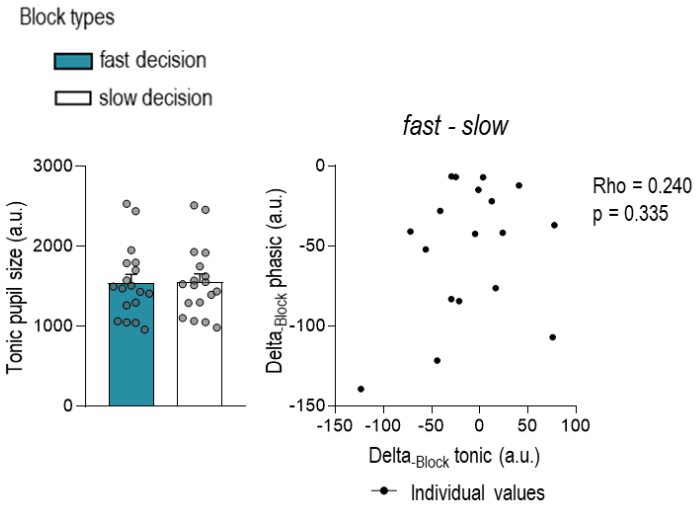

Figure S5. Tonic pupil dilation in Experiment 1 (n=18). As a control analysis, we considered a window of 250 ms before the trial onset to measure tonic pupil dilation. As shown on the left panel, such tonic pupil dilation was similar in fast (blue bar) and slow decision blocks (white bar). Furthermore, block-related changes in tonic dilation (Delta$_{\text{-Block}}$ tonic) did not correlate significantly with changes in Peak pupil dilation (Delta$_{\text{-Block}}$ phasic), ruling out the possibility that a difference in baseline (tonic) pupil between the two block types could have been responsible for our results on phasic pupil size (right panel).

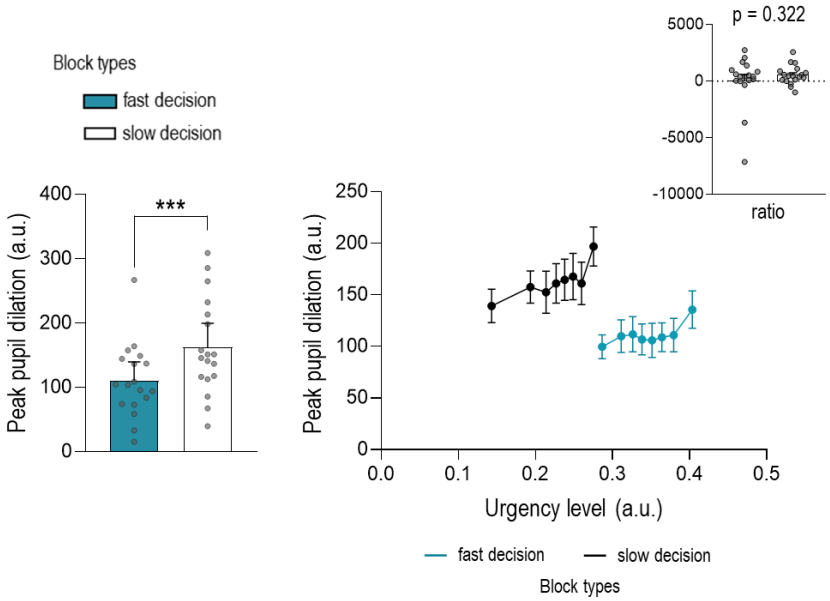

Figure S6. Peak pupil data as a function of urgency at decision time in Experiment 1 (n=18). Peak pupil dilation was smaller in fast (blue bar) than slow (white bar) decision blocks (left panel). Consistent with the positive correlation found between pupil dilation and urgency signal, Peak pupil dilation increased with urgency level in both types of blocks (right panel). Furthermore, this increase in pupil dilation with urgency was similar between the two block types as emphasize by the similar ratios ($Delta_{-Bin}$ pupil/$Delta_{-Bin}$ urgency; see inset). Error bars represent SE. ***p < 0.001.

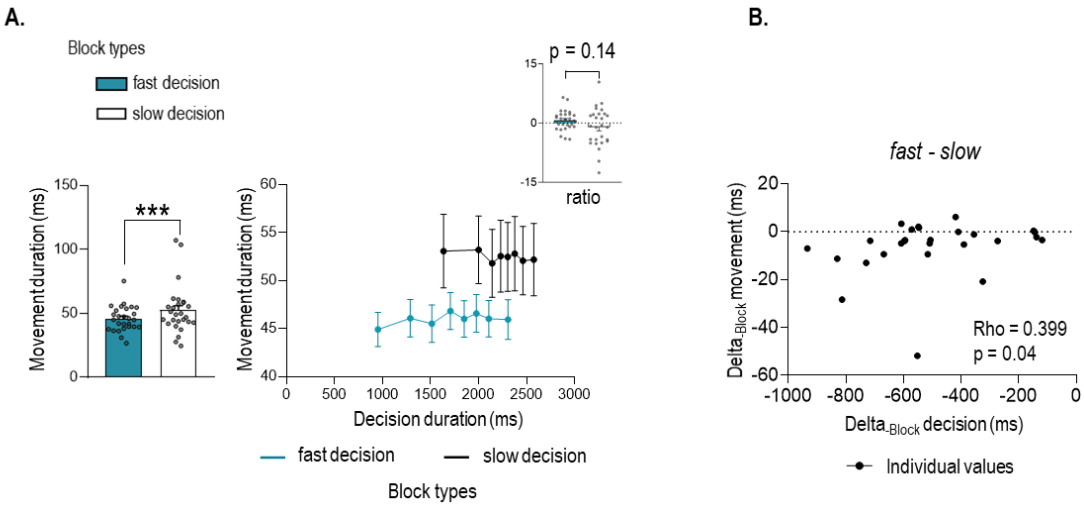

Figure S7. Impact of decision duration on movement duration in Experiment 1, focusing on the subjects who were part of the slow decision group in Experiment 2 (n=27). This group of subjects showed a tradeoff type of relationship between decision and movement duration in Experiment 2. Here, we verified that their performance in Experiment 1 supported a coregulation between these two levels of control. As depicted in **A.**, the results showed faster movements in fast decision (blue bar) relative to slow decision (white bar) blocks (left panel). Moreover, the duration of movements as a function of decision duration evolved differently between the two types of blocks (right panel). Although the ratios did not differ from 0 for both fast and slow decision blocks (see inset), the ratio for slow decision blocks still tended to be lower. Regarding the correlation (**B.**), we found a positive correlation between the change between fast and slow decision blocks in decision duration ($Delta_{-Block}$ decision) and movement duration ($Delta_{-Block}$ movement); the more participants responded faster in fast decision blocks compare to slow ones (i.e., lower $Delta_{-Block}$ decision values), the more they accelerated their movement speed (i.e., lower $Delta_{-Block}$ movement values) in this block type. Hence, subjects in the slow decision group switched from displaying a coregulation between decision and movement in Experiment 1 to a tradeoff relationship in Experiment 2. Error bars represent SE. ***p < 0.001.

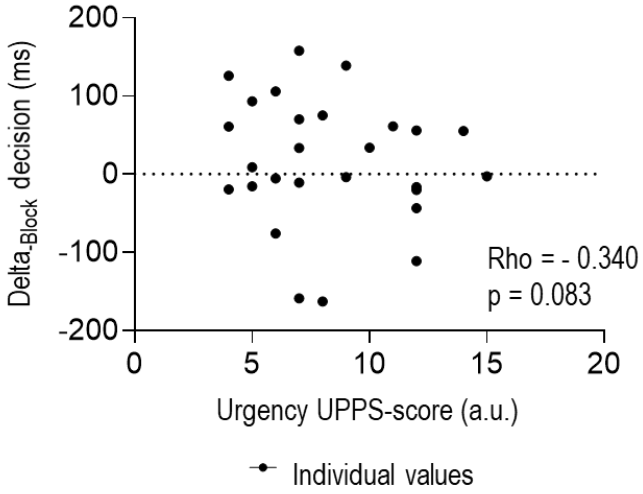

Figure S8. Correlation with UPPS-score in slow decision group of Experiment 2. Given that deltas were computed by measuring the difference in duration between fast and slow conditions, the more the subjects showed an effect of the condition (or tradeoff), the more they displayed a positive $Delta_{-Block}$ decision**.** Subjects who were more impulsive (higher Urgency UPPS-score) tended to show less ability to slow down (lower $Delta_{-Block}$ decision).

	Fast decision	*Slow decision*	*BF_{10}*	*Error %*
gender (M/F)	12/15	10/17	0.309	0.008
Age	25.11 ± 3.65	23.81 ± 2.87	0.651	0.008
Urgency	8.52 ± 3.19	8.37 ± 3.20	0.277	0.008
Positive urgency	10.63 ± 2.82	10.56 ± 1.85	0.275	0.008
Lack of Perseverance	7.85 ± 2.52	7.30 ± 2.45	0.361	0.008
Lack of Premeditation	6.70 ± 2.46	7.33 ± 2.45	0.396	0.008
Sensation seeking	11.07 ± 2.05	10.33 ± 3.06	0.430	0.008

Table S1. Demographic description of fast decision and slow decision groups. The table includes the Bayesian independent t-tests for the sex, the age and the five facets of trait impulsivity of the short-UPPS. BF_{10} grades the strength of evidence for the alternative hypothesis against the null hypothesis. The error percentage (Error %) indicates the numeric robustness of the results, with low values of the Error % corresponding to a greater numerical stability of results. The gender of the participants was transformed into a numerical score to compare the average between the two groups (i.e., 1 for female (F) and 0 for male (M)).

Bin_{DD}	*t-value*	*df*	*p-value*	*Cohen's d*
1	**12.784**	**55**	**< 0.001**	**1.708**
2	**10.122**	**55**	**< 0.001**	**1.353**
3	**8.298**	**55**	**< 0.001**	**1.109**
4	**7.261**	**55**	**< 0.001**	**0.970**
5	**6.421**	**55**	**< 0.001**	**0.858**
6	**5.676**	**55**	**< 0.001**	**0.758**
7	**4.816**	**55**	**< 0.001**	**0.644**
8	**3.761**	**55**	**< 0.001**	**0.503**

Table S2. Paired Student's t-tests of urgency level over decision duration in Experiment 1. The table presented a comparison of the level of urgency between fast decision blocks and slow decision blocks across each of the 8 decision duration bins (Bin_{DD}). For every bin, the level of urgency was significantly higher in the fast than in the slow decision blocks. The critical t-value, the p-value and the Cohen's d as a measure of the effect size are represented for each Bin_{DD}. Significant p-value (with a Bonferroni-corrected threshold of .05/8) are highlighted in bold and blue.

Bin_{DD}	*t-value*	*df*	*p-value*	*Cohen's d*
1	-3.086	17	0.007	-0.727
2	**-4.007**	**17**	**< 0.001**	**-0.944**
3	-2.352	17	0.031	-0.554
4	**-3.561**	**17**	**0.002**	**-0.839**
5	**-4.408**	**17**	**< 0.001**	**-1.039**
6	**-3.884**	**17**	**0.001**	**-0.915**
7	**-3.191**	**17**	**0.005**	**-0.752**
8	**-5.583**	**17**	**< 0.001**	**-1.316**

Table S3. Paired Student's t-tests of pupil dilation over decision duration in Experiment 1. The table presented a comparison of the pupil dilation between fast decision blocks and slow decision blocks across each of the 8 decision duration bins (Bin_{DD}). Supporting the BlockType x decision duration interaction in the mixed model (see related section in Analyses of pupil dilation for more details), the paired t-tests showed that, in early bins, pupil dilation did not differ significantly between block types but that it became progressively larger in slow than fast decision blocks in the last bins of decision duration. The critical t-value, the p-value and the Cohen's d as a measure of the effect size are represented for each Bin_{DD}. Significant p-value (with a Bonferroni-corrected threshold of .05/8) are highlighted in bold and blue.

Chapter 2: Post-error slowing reflects the joint impact of adaptive and maladaptive processes during decision making

Published in Frontiers in Human Neuroscience 2022.

Fanny Fievez[1]*, Gerard Derosiere[1], Frederick Verbruggen[2], Julie Duque[1]

Author affiliations: *[1] Institute of Neuroscience, Université Catholique de Louvain, 1200, Brussels, Belgium. [2] Department of Experimental psychology, Ghent University, 9000 Gent, Belgium*

Abtract: Errors and their consequences are typically studied by investigating changes in decision speed and accuracy in trials that follow an error, commonly referred to as “post-error adjustments”. Many studies have reported that subjects slow down following an error, a phenomenon called “post-error slowing” (PES). However, the functional significance of PES is still a matter of debate as it is not always adaptive. That is, it is not always associated with a gain in performance and can even occur with a decline in accuracy. Here, we hypothesized that the nature of PES is influenced by one’s speed-accuracy tradeoff policy, which determines the overall level of choice accuracy in the task at hand. To test this hypothesis, we had subjects performing a task in two distinct contexts (separate days), which either promoted speed (hasty context) or cautiousness (cautious context), allowing us to consider post-error adjustments according to whether subjects performed choices with a low or high accuracy level, respectively. Accordingly, our data indicate that post-error adjustments varied according to the context in which subjects performed the task, with PES being solely significant in the hasty context (low accuracy). In addition, we only observed a gain in performance after errors in a specific trial type, suggesting that post-error adjustments depend on a complex combination of processes that affect the speed of ensuing actions as well as the degree to which such PES comes with a gain in performance.

4.1. Introduction

We all make mistakes. For instance, many of us have experienced sending an email to the wrong person. After such an error, we typically write a second message to apologize and rectify. But when we send the second email, we usually take more time to check that the recipient is correct. We therefore adapt our behavior in order to avoid reproducing previous mistakes. Such an ability to adapt after an error is essential to achieve our goals.

Errors and their consequences are typically studied in two-choice reaction time tasks by investigating changes in decision speed and accuracy in trials that follow an error, commonly referred to as “post-error adjustments”. Using such tasks, many studies have reported that subjects slow down following an error, a phenomenon called “post-error slowing” (PES) (Dubravac et al., 2020; Fu et al., 2019; Nigbur & Ullsperger, 2020; Topor et al., 2021).

The functional significance of PES is still a matter of debate though (Damaso et al., 2020; Kirschner et al., 2021; Wessel, 2018). Because slowing down after an error is often associated with an increase in accuracy, PES is traditionally attributed to adaptive adjustments of decision policies, favoring a more cautious response style to improve performance in the subsequent trial (Beatty et al., 2020; Cavanagh et al., 2014; Purcell & Kiani, 2016; Rabbitt & Vyas, 1970; Siegert et al., 2014; Smith & Brewer, 1995; Steinhauser & Andersen, 2019). However, several recent studies have revealed that PES can also occur in a somewhat ‘maladaptive’ way as, sometimes, slowing does not necessarily lead to improvement in accuracy; in fact, PES can even come with a decrease in decision accuracy (Ceccarini et al., 2019; Compton et al., 2021; Eben et al., 2020b; Kirschner et al., 2021; Schroder et al., 2020; Smith et al., 2020). These findings

indicate that the functional significance of PES may vary according to the context in which it is observed.

A careful analysis of the literature reveals that the degree to which PES is adaptive (i.e., increases accuracy) or 'maladaptive' (i.e., takes place without accuracy improvement) depends partly on the average level of accuracy of subjects in the task at play. That is, in studies reporting an adaptive PES, the overall level of choice accuracy is typically low (i.e., generally between 60 - 80% of correct choices) because the task is relatively complex and/or because the instruction requires subjects to respond quickly within a given time limit (Purcell & Kiani, 2016; Siegert et al., 2014; Steinhauser & Andersen, 2019). In this situation, errors are clearly expected and slowing down after them has a positive effect on choice accuracy (Damaso et al., 2020; Dyson et al., 2018; Hajcak et al., 2003; Siegert et al., 2014; Wessel, 2018). By contrast, studies reporting a maladaptive PES rather use reaction time tasks that are quite simple such that the overall level of choice accuracy is usually much higher (i.e., more between 80 – 100% of correct choices) (Castellar et al., 2010; Compton et al., 2021; Eben, Billieux, & Verbruggen, 2020; Houtman et al., 2012; Kirschner et al., 2021; Li et al., 2020; Notebaert et al., 2009). In such settings, errors represent infrequent and unexpected events that may catch attention, resulting in a maladaptive PES that deteriorates (rather than enhances) choice accuracy in the consecutive trial (Castellar et al., 2010; Houtman et al., 2012; Sokolov, 1963).

Thus, whether PES is adaptive or maladaptive might be partly influenced by choice accuracy. This in turn depends on the task characteristics, such as its global difficulty or on the speed-accuracy tradeoff (SAT) policy of subjects performing the task. Indeed, most decisions require balancing speed and accuracy, making the SAT a

universal property of behavior (Guo et al., 2020; Henmon, 1911; Miletić et al., 2021; Reynaud et al., 2020; Rinberg et al., 2006; Salinas et al., 2014). Humans and other non-human animals are able to adjust their SAT depending on context, favoring either hasty (i.e., high speed, low accuracy) or cautious (i.e., low speed, high accuracy) decision policies (Chittka et al., 2009; Heitz, 2014; Spieser et al., 2017; Thura, 2020). Hence, because choice accuracy varies depending on the SAT, it is plausible that PES can shift from being adaptive to being maladaptive depending on whether the emphasis is on speed or accuracy when performing the same task in separate blocks.

In conclusion, past research suggests that errors can trigger PES of adaptive or maladaptive nature (Joram van Driel et al., 2012; Schiffler et al., 2017; Wessel, 2018). These two different types of behavior have been evidenced in separate studies using distinct tasks or instructions where performance is either characterized by a low or a high level of choice accuracy, respectively. Here, we hypothesized that the nature of PES can also vary within a given task depending on whether the SAT context favors a hasty (i.e., high speed, low accuracy) or a cautious (i.e., low speed, high accuracy) decision policy. More precisely, we predicted that errors would be common and expected when the context favors choice speed due to the choices' promptness (Damaso et al., 2020), whereas they would be rare and unexpected when the context favors choice accuracy. Hence, we expected PES to be less adaptive (and potentially maladaptive) when the emphasis is on choice accuracy in a cautious SAT context compared to when the emphasis is on response speed. To test this hypothesis, we used a modified version of the "Tokens task" (Cisek et al., 2009; Derosiere et al., 2019, 2021), involving choices between left and right index fingers. In this task, incorrect choices led either to a low or to a high penalty in two different SAT contexts, inciting subjects

to implement either hasty or cautious decision policies, respectively. We predicted that PES would be more adaptive (i.e., associated with a higher increase in accuracy) in the low than in the high penalty context.

4.2. Material and Method

Participants

A total of 43 healthy volunteers participated in this study (25 Women: 23.5 ± 2.3 years old). All participants were right-handed according to the Edinburgh Questionnaire (Oldfield, 1971). None of them had any neurological disorder or history of psychiatric illness or drug or alcohol abuse; and no one was following any clinical treatment that could have influenced performance. Participants were financially compensated for their participation and could also receive extra compensation based on their performance on the task (see below). All gave written informed consent at the beginning of the experiment. The protocol was approved by the Ethics Committee of the Université catholique de Louvain (UCLouvain), Brussels, Belgium. Data presented here were also used (for a different purpose) in another paper (Derosiere et al., 2022).

Tokens task

Subjects were seated in front of a computer screen, positioned at a distance of 70 cm from their eyes. Both forearms were placed on the surface of a table with the left and right index fingers placed on a keyboard turned upside down (Fig. 1.A). Subjects performed a variant of the “Tokens task” (Cisek et al., 2009; Derosiere et al., 2021; Thura & Cisek, 2014), which was implemented by means of LabView 8.2 (National Instruments, Austin,TX). In this decision making task, participants had to continuously monitor the distribution of 15 tokens

jumping one by one from a central circle to one of two lateral circles. The subjects were instructed to guess which lateral circle would ultimately receive the majority of the tokens; they had to indicate their choice before the last token jump, by pressing a key with the left or right index finger (i.e., a F12 or F5 key-press for the left or right circle, respectively).

As depicted on Figure 1.A., in between trials, subjects were always presented with a default screen, consisting of three blue circles (4.5 cm diameter each) displayed on a white background for 2500 ms. Each trial started with the appearance of the 15 tokens randomly arranged in the central circle. After a delay of 800 ms, a first token jumped towards the left or right circle, followed every 200 ms, by the other tokens, jumping one by one, to one of the two lateral circles. Subjects were asked to respond as soon as they felt sufficiently confident. The reaction time (RT) was calculated by computing the difference between the time at which subjects pressed the key to indicate their choice and the time of the first tokens jump ($Jump_1$). After subjects had pressed the corresponding key, the tokens kept jumping every 200 ms until the central circle was empty (i.e., 2800 ms after $Jump_1$). So, the feedback appeared only once all tokens were distributed. At this time, the chosen circle was highlighted either in green or in red depending on whether the response was correct or not, respectively. In addition, a numerical score displayed above the central circle provided subjects with a feedback of their performance (see the ‘Reward, penalty and SAT contexts’ section below). In the absence of any response before the last jump, the central circle turned red with a “Time Out” message and a “-4” (score) appeared on top of the screen. The feedback screen lasted for 500 ms and then disappeared at the same time as the tokens did (the circles always remained on the screen), denoting the end of the trial. From the

appearance of the tokens in the central circle, each trial lasted for 6600 ms.

One key feature of the tokens task is that it allows one to calculate, in each trial, the “success probability” pi(t) associated with choosing the correct circle i at each moment in time t. For example, for a total of 15 tokens, if at a particular moment in time the right (R) circle contains NR tokens, the left (L) circle contains NL tokens, and the central (C) circle contains NC tokens, then the probability that the circle on the left will ultimately be the correct one (i.e., the success probability of guessing left) is described as follows, where k represents the number of elements in the summation component of the equation :

$$p(L \mid NL, NR, NC) = \frac{NC!}{2^{NC}} \sum_{k=0}^{\min(NC,7-NR)} \frac{1}{k!(NC-k)!} \quad (1)$$

Although the token jumps appeared completely random to subjects, the direction of each jump was determined a priori, producing different types of trials according to specific temporal profiles of pi(t). There were four trial types: ambiguous, obvious, misleading, and arbitrary. The majority of trials (60 %) were ambiguous, as the initial jumps were balanced between the lateral circles, keeping the pi(t) close to 0.5 until late in the trial (i.e., pi(t) remained between 0.5 and 0.66 up to the $Jump_{10}$). 15 % of trials were “obvious”, meaning that the initial token jumps consistently favored the correct circle (i.e., pi(t) was already above 0.7 after $Jump_3$ and above 0.8 after $jump_5$). 15% of the trials were “misleading”, where most of the first token jumps occurred towards the incorrect lateral circle (i.e., pi(t) remained systematically below 0.4 until $Jump_3$; from then on, the following tokens jumped mainly in the other direction, that is, towards the circle that eventually turned out being correct). Finally, we included 10 % of trials that were

completely arbitrary. These different types of trials were always presented in a randomized order.

Reward, penalty and SAT contexts

As mentioned above, at the end of each trial, subjects received a feedback score. Correct responses led to a positive score (i.e., a reward) while incorrect responses led to a negative score (i.e., a penalty). Subjects were told that the sum of these scores would turn into a monetary reward at the end of the experiment.

In correct trials, the reward corresponded to the number of tokens remaining in the central circle at the time of the response (in € cents). Hence, reward for a correct choice in a given trial gradually decreased over time (Fig. 1.B.). For instance, a correct response provided between $Jump_5$ and $Jump_6$ led to a gain of 10 cents (10 tokens remaining in the central circle). However, it only led to a gain of 5 cents when the response was provided between $Jump_{10}$ and $Jump_{11}$ (5 tokens remaining in the central circle). Hence, using a reward dropping over time increased time pressure over the course of a trial and pushed subjects to respond as fast as possible (Derosiere et al., 2019, 2022).

The penalty provided for incorrect choices did not depend on the time taken to choose a lateral circle. Importantly though, it differed between two contexts. In a first context, the cost of making an incorrect choice was low as the penalty was only of -4 cents, pushing subjects to make hasty decisions in order to get high reward scores (hasty context). Conversely, incorrect choices were severely sanctioned in the second context as the penalty there was of -14 cents, emphasizing the need for cautiousness (cautious context).

Moreover, not providing a response before $Jump_{15}$ (i.e., time out trials) also led to a penalty, which was of -4 cents both in the hasty and in the cautious contexts. Hence, in the hasty context, providing an incorrect response or not responding led to the same penalty (i.e., -4 cents), further increasing the urge to respond before the end of the trial in this context. Conversely, in the cautious context, the penalty for making an incorrect choice was much higher than that obtained for an absence of response (i.e., -14 vs -4 cents, respectively), further increasing subjects' cautiousness in this context.

Hence, with these two contexts, we could consider post-error behavioral adjustments depending on whether the cost of errors was either low or high, prompting the subjects to put the emphasis on decision speed (low accuracy) or on decision accuracy (high accuracy), respectively. As mentioned above, we expected to observe a post-error slowing (PES) in both cases but predicted that it would be more adaptive in the hasty than in the cautious blocks.

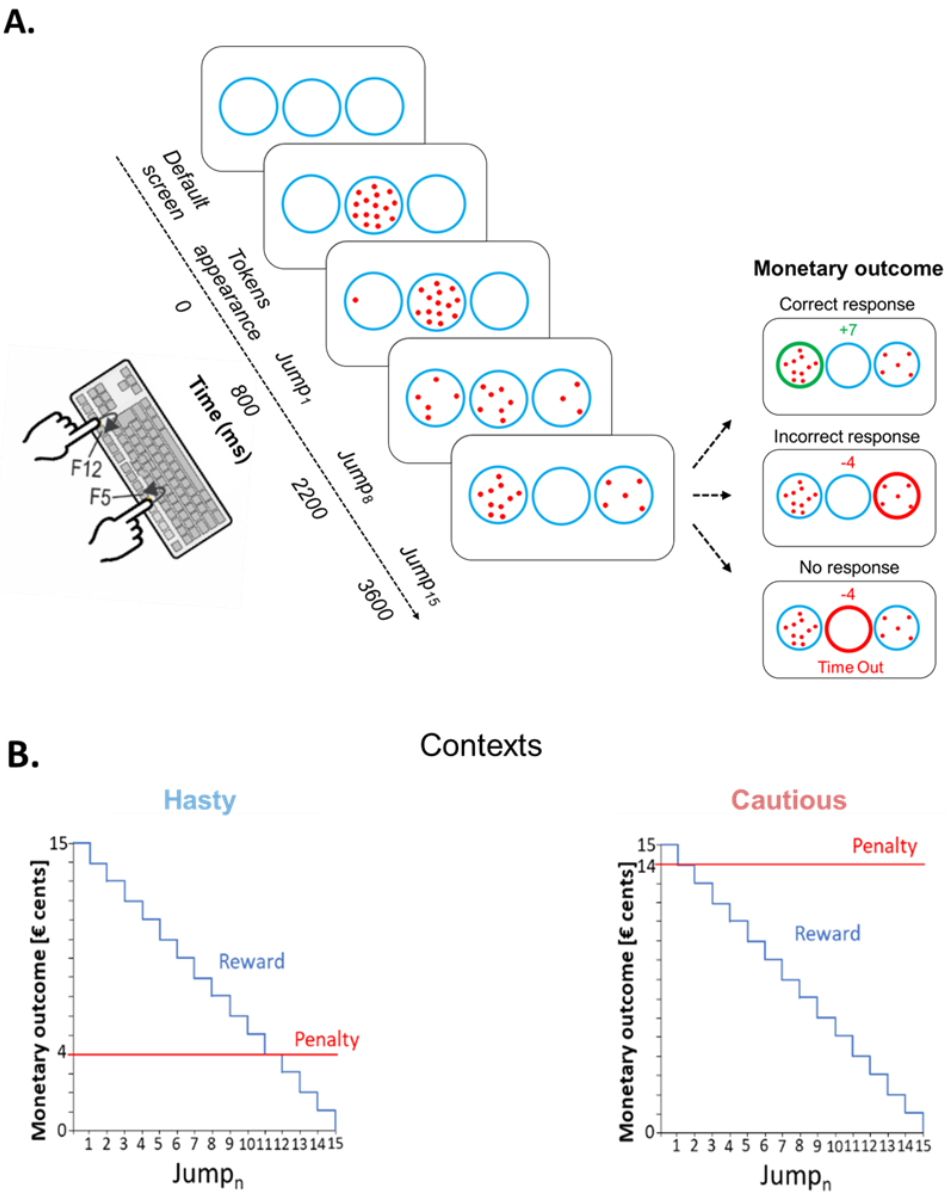

Figure 1. A. Schematic of the Tokens task. In each trial, 15 tokens jumped one-by-one every 200 ms from the central circle to one of the lateral circles. The subjects had to indicate by a left or right index finger keypress (i.e., F12 and F5 keys, respectively) which lateral circle they thought would receive the majority of tokens at the end of the trial. For a correct response, the subjects won, in € cents, the number of tokens remaining in the central circle at the time of the response. Hence, the reward earned for a correct response decreased over time, as depicted in B. The right side of panel A depicts the monetary outcome in three exemplary cases. The upper inset represents the reward provided for a correct response between $Jump_8$ and $Jump_9$, that is when 7 tokens remain in the central circle at the moment the left circle is chosen; the middle

inset represents the penalty for an incorrect response in the hasty context, fixed at -4 cents; the lower inset shows the penalty in a “Time Out” trial (no response), fixed at -4 cents, regardless of the context. For representative purposes, the “Time Out” message is depicted below the circles in this example, while it was presented on top of the screen in the actual experiment. **B. Contexts**. Incorrect responses led to a fixed negative score, which differed depending on the context. In the hasty context (shown on the left), the penalty was low, equaling only 4 cents (see red line), promoting fast decisions. In contrast, in the cautious context (shown on the right), the penalty was high, equaling 14 cents, promoting thus slower decisions.

Sensory evidence at RT

The Tokens task also allowed us to assess the amount of sensory evidence (i.e., available information) supporting the subjects’ choice at the RT. To estimate the level of sensory evidence at RT, we computed a first-order estimation as the sum of log-likelihood ratios (SumLogLR) of individual token movements at this time (Cisek et al., 2009):

$$SumLogLR(n) = \sum_{k=1}^{n} \log(\frac{p(e_k \mid S)}{p(e_k \mid NS)} \quad (2)$$

In this equation, $p(e_k|S)$ is the likelihood of a token event e_k (a token jumping into either the chosen or unchosen lateral circle) during trials in which the chosen circle S is correct, and $p(e_k|NS)$ is its likelihood during trials in which the unchosen circle NS is correct. K, here, represents the different token jumps. The SumLogLR is proportional to the difference between the number of tokens contained in each lateral circle; the larger the number of tokens in the chosen circle, as compared to the unchosen circle, the higher is the evidence for the choice and thus the SumLogLR (Derosiere et al., 2019). We expected the latter to be overall higher in the cautious than in the hasty context, reflecting the higher evidence needed before committing to an accurate choice in the former context (Heitz, 2014; Miletić et al., 2021; Ratcliff, 2002).

Experimental procedure

Subjects performed the task in the two contexts in two different experimental sessions conducted on separate days at a 24-h interval. The order of the two sessions (i.e., hasty and cautious) was counterbalanced across participants. As described below, each session involved the same structure, except for the addition of a familiarization block in the first session only, to allow subjects to become acquainted with the basic principles of the task (this was of course not necessary for the session coming on the second day).

Each session started with two short blocks involving a simple reaction time (SRT) task. This task was similar to the Tokens task described above except that, here, all tokens jumped simultaneously into one of the two lateral circles. The subjects were instructed to respond as fast as possible by pressing the appropriate key (i.e., F12 or F5 for the left or the right circle, respectively). In a given SRT block, the tokens jumped always into the same circle, and subjects were informed in advance of the circle to choose within a block. This SRT task allowed us to estimate the sum of the delays attributable to the sensory and motor processes in the absence of a choice, as achieved in past studies (Cisek et al., 2009; Thura et al., 2014).

Then, subjects performed a few practice blocks. The first one (10 trials) consisted in a version of the Tokens task in which the feedback was simplified; indicating only if the subjects' choice was correct or incorrect by highlighting the chosen circle in green or red, respectively; no reward or penalty was provided here. This first practice block served to familiarize subjects with the basic aspects of the task and was only used during the first session. The practice then continued with two blocks (20 trials each) where subjects performed

the task in the context they would be involved in for the whole session (hasty or cautious blocks).

After that, the actual experiment involved 8 blocks of 40 trials (320 trials per session; 640 trials per subject). Each block lasted about 4 min and a break of 2 to 5 minutes was provided between each block. Each session lasted approximatively 150 minutes.

Statistical analyses

The analyses comprised two parts: first, we ran some tests to check that our manipulation of the penalty indeed led the subject to adopt different SAT policies in the two contexts. Second, and more related to the goal of the current study, we performed analyses to compare the post-error adjustments in the two contexts. Most of the statistical comparisons involved repeated-measures analyses of variance ($ANOVA_{RM}$) run with the Statistica software (version 10.0, Statsoft, Oklahoma United-States). Post-hoc comparisons were conducted using the Tukey's Honestly Significant Difference (HSD) procedure. The significance level was set at $p < .05$. Moreover, for the analyses regarding post-error adjustments, we ran a Bayesian equivalent of the $ANOVA_{RM}$ (and t-tests) with JASP (Wagenmakers, Love, et al., 2018). In this case, the Bayes Factor (BF_{10}) quantifies the evidence for the alternative hypothesis against the null hypothesis and the prior and posterior inclusion probabilities (P(incl) et P(incl|data)) refer to the importance of each parameter based on the prior and posterior probabilities of each model including it, respectively. All data are presented as mean ± SE.

Manipulation check

In order to verify that our manipulation of penalty (-4 or -14 cents) successfully induced SAT adaptations, we considered the RT,

the percentage of correct choices (%Correct) and the SumLogLR at RT in the two contexts. Overall, we expected to observe larger values for these variables in the high penalty (-14 cents) than in the low penalty (-4 cents) blocks, supporting a more conservative behavior in the cautious context compared to the hasty one. To address this directly, we analyzed each variable using two-way ANOVAs$_{RM}$ with CONTEXT (hasty or cautious) and TRIAL_TYPE (obvious, ambiguous or misleading) as within-subject factors.

Post-error adjustments

All analyses on post-error adjustments focused on behavior in ambiguous trials. This allowed us to characterize post-error adjustments in a homogeneous set of (ambiguous) trials. We investigated behavior in these trials, referred to as the "n" trials (trials$_n$), according to whether they followed an error or a correct choice. These trials preceding trials$_n$ are referred to as trial$_{n-1}$ and were separated according to whether they were ambiguous or misleading; there were too few errors in obvious trials to consider them as trials$_{n-1}$. Thus, we considered post-error adjustments on ambiguous trials$_n$ according to the type of trials$_{n-1}$ (ambiguous or misleading). For this analysis, we had to exclude 14 participants who had less than five trials$_n$ in at least one of the experimental conditions. As a result, statistical analyses were run on a total of 29 subjects (17 women: 23.4 ± 2.4 years old). On average in the hasty context, we characterized adjustments following errors in 22 ± 8 ambiguous trial$_{n-1}$ and 15 ± 6 misleading trial$_{n-1}$ (corresponding to an error rate of 21 ± 7% and 44 ± 18%, respectively). In the cautious context, errors occurred in 13 ± 5 ambiguous trials$_{n-1}$ and 10 ± 4 misleading trial$_{n-1}$ (corresponding to an error rate of 13 ± 5% and 30 ± 12%, respectively).

There are different methods for quantifying post-error adjustments in $trials_n$ (Dutilh et al., 2012; Hajcak & Simons, 2002). In the present study, we used a traditional approach consisting in calculating deltas (Δ) for the RT (ΔRT, ms) and for the %Correct (Δ%Correct) in $trials_n$ as follows: ΔRT was obtained by calculating the difference between the RT in correct $trials_n$ that either followed an error or a correct choice in $trials_{n-1}$ (Damaso et al., 2020; Smith et al., 2020; Williams et al., 2016). Similarly, Δ%Correct corresponded to the difference in %Correct between $trials_n$ following an error or a correct choice in $trials_{n-1}$. Hence, PES manifests as a positive ΔRT. If this positive ΔRT is associated with a positive Δ%Correct, it means that the PES is adaptive (i.e., is associated with a gain in decision accuracy) while a null or negative Δ%Correct reflects a maladaptive PES (no gain or drop in decision accuracy). These ΔRT and Δ%Correct were analyzed using two-ways $ANOVA_{RM}$ with CONTEXT (hasty or cautious) and $trials_{n-1}$-TYPE (ambiguous or misleading) as within-subject factors.

4.3. Results

Manipulation check

On average, subjects displayed RTs of 1866 ± 457 ms; they performed with a %Correct of 81 ± 18 %, and did so for a level of evidence corresponding to 0.35 ± 0.72 (SumLogLR at RT value; a.u.). Importantly, as depicted in Figure 2 (upper panel), all these values were lower when the penalty was low (i.e. equal to -4 cents) compared to when it was high (i.e. equal to -14 cents), supporting a shift from a cautious to a hasty response policy when the penalty was low (all CONTEXT $F_{1,28} > 7.3$, all $p < .05$, see Table 1).

In addition, as shown on the lower panel of Figure 2, the $ANOVA_{RM}$ revealed an effect of the TRIAL_TYPE on all three parameters (all $F_{2,56} > 222$, $p < .001$). As expected, subjects responded faster and more accurately in the obvious trials than in the other trials (all $p < .001$). They were also faster in misleading than in ambiguous trials ($p < .001$) but showed a lower accuracy (i.e., lower %Correct) in the former trial type ($p < .001$), consistent with their misleading nature. Regarding the SumLogLR at RT, it was the highest in the obvious and the lowest in the ambiguous trials (all $p < .001$), consistent with the different predefined pattern of token jumps in these different trial types.

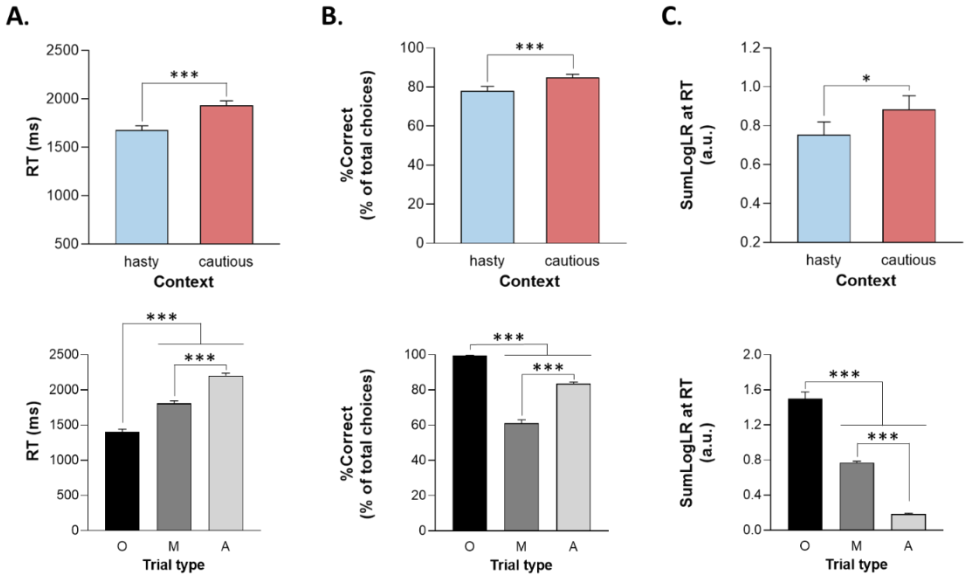

Figure 2: Reaction time (A; RT), percentage of correct choices (B; %Correct) and sensory evidence at RT (C; SumLogLR at RT), depending on the context (upper panel; hasty or cautious) and the trial type (lower panel; Obvious (O), Misleading (M) or Ambiguous (A)). Error bars represent SE. *p < .05, ***p < .001: significantly different.

Finally, the RT and SumLogLR at RT did not display any significant CONTEXT x TRIAL_TYPE interaction (all $F_{2,56} < 2.8$, all $p > .05$). Yet, as depicted in Figure 3, this interaction was significant for the %Correct ($F_{2,56} = 14.35$, $p < .001$). As such, the %Correct was larger in the cautious context relative to the hasty one but only in ambiguous and misleading trials ($p < .01$ and $p < .001$, respectively). In fact, the obvious trials were so easy that subjects did not make mistakes in this trial type whatever the context.

	FACTOR	MES	F-value	p-value	η_P^2
RT	CONTEXT	2903696	33.667	**< .001**	.987
	TRIAL_TYPE	9316608	385.188	**< .001**	.546
	CONTEXT X TRIAL_TYPE	6143	.582	.562	.932
%CORRECT	CONTEXT	2117	41.31	**< .001**	.999
	TRIAL_TYPE	21663	222.91	**< .001**	1
	CONTEXT X TRIAL_TYPE	655	14.35	**< .001**	.998
SUMLOGLR AT RT	CONTEXT	.745	7.349	**.011**	.208
	TRIAL_TYPE	25.172	222.121	**< .001**	.888
	CONTEXT X TRIAL_TYPE	.260	2.728	.074	.089

Table 1. Inferential analyses of behavioral adaptations to the SAT context. The main error square (MES), critical F-value, p-value and partial eta-squared (η_P^2) are provided for each factor (CONTEXT; TRIAL_TYPE) and their interaction (CONTEXT X TRIAL_TYPE), following the analysis of reaction time (RT), percentage of correct choices (%Correct) and sensory evidence at RT (SumLogLR at RT). Significant p-values are highlighted in bold and blue

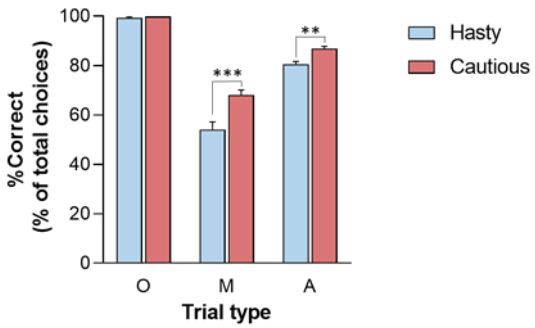

Figure 3: CONTEXT x TRIAL_TYPE interaction on percentage of correct choices (%Correct). %Correct was lower in the hasty (blue bars) than in the cautious (red bars) context when considering Misleading (M) and Ambiguous (A) trials but not for the Obvious (O) trials. Note the absence of errors in these latter trials (%Correct=100), whether in the hasty or cautious context. **p < .01, ***p < .001: significantly different.

Post-error adjustments

Post-error adjustments (ΔRT and Δ%Correct), calculated with the traditional approach (Dutilh et al., 2012), are displayed in Figure 4 for $trials_n$ (always ambiguous), following either ambiguous or misleading $trials_{n-1}$. Even if ΔRT values were positive in all conditions, which would be consistent with the occurrence of PES, Student's t-tests against 0 showed that this slowdown was only significant in the hasty context (ΔRT significantly above 0 with a Bonferroni-corrected threshold of .05/4), regardless of the $TRIAL_{n-1}$_TYPE (both $t_{29} > 3$, p = [.0003 .005], Cohen's *d* = [.567 .767]); t-tests did not reveal any significant difference between ΔRT and 0 in the cautious context (both $TRIAL_{n-1}$_TYPE $t_{29} > .8$, p = [.024 .401], Cohen's *d* = [.158 .444]). Similarly, equivalent Bayesian analyses (Wagenmakers, Love, et al., 2018) showed moderate to strong evidence for PES in the hasty context (BF_{10} = [8.330 98.677]), and moderate evidence for a lack of adjustment after an error in the caution context (BF_{10} = [.275 2.207]). Consistently, the $ANOVA_{RM}$ revealed a significant effect of CONTEXT on ΔRT ($F_{1,28}$ = 6.26, p = .018), in the absence of $TRIAL_{n-1}$_TYPE effect

($F_{1,28}$ = .49, p = .49) or CONTEXT x $TRIAL_{n-1}$_TYPE interaction ($F_{1,28}$ = 1.39, p = .25). These results were supported by a Bayesian analysis showing moderate evidence for a context effect (BF_{10} = 5.411, see Table 2).

	FACTOR	P(incl)	P(incl|data)	BF_{incl}	BF_{10}	η_P^2
ΔRT	CONTEXT	.600	.853	3.854	**5.411**	.183
	$TRIAL_{n-1}$_TYPE	.600	.247	.219	.255	.17
	CONTEXT X $TRIAL_{n-1}$_TYPE	.200	.065	.278	.553	.05
Δ%Correct	CONTEXT	.600	.322	.317	.348	.051
	$TRIAL_{n-1}$_TYPE	.600	.626	1.116	**1.444**	.112
	CONTEXT X $TRIAL_{n-1}$_TYPE	.200	.078	.341	.283	.050

Table 2. Inferential analyses of behavioral changes in $trial_n$. The prior inclusion probability P(incl), the posterior inclusion probability P(incl|data) and the change from prior to posterior inclusion odds (BF_{incl}) are provided for each factor (CONTEXT; $TRIAL_{n-1}$_TYPE) and their interaction (CONTEXT X $TRIAL_{n-1}$_TYPE), following the analysis of reaction time and %Correct change in $trial_n$ (ΔRT and Δ%Correct). In addition, the BF_{10} grades the strength of evidence for the alternative hypothesis against the null hypothesis and the partial eta-squared (η_P^2) represents a measure of the effect size. BF_{10} revealing a significant factor effect are highlighted in bold and blue.

Figure 4 (lower panel) evokes positive Δ%Correct in all conditions, which would indicate an increase in decision accuracy in $trial_n$. Yet, the Student's t-tests showed that, this effect was only significant in the hasty context; more surprisingly, it was only present following misleading $trials_{n-1}$ (t_{29} = 4.21, p < .001, Cohen's *d* = .781 and BF_{10} = 118.923; Bonferroni-corrected threshold= .05/4, see Table 3 for more details). Note though that the variations in Δ%Correct between the different conditions were rather weak, as confirmed by the $ANOVA_{RM}$ analyses which only revealed a marginal effect of $TRIAL_{n-1}$_TYPE ($F_{1,28}$ = 3.53, p = .07), with no effect of CONTEXT ($F_{1,28}$ = 1.51, p = .23) or CONTEXT x $TRIAL_{n-1}$_TYPE interaction ($F_{1,28}$ = 1.48, p = .23 and BF_{10} = .283). These results were supported by a Bayesian

analysis showing anecdotal evidence for a $TRIAL_{n-1}$_TYPE effect (BF_{10} = 1.444, see Table 2).

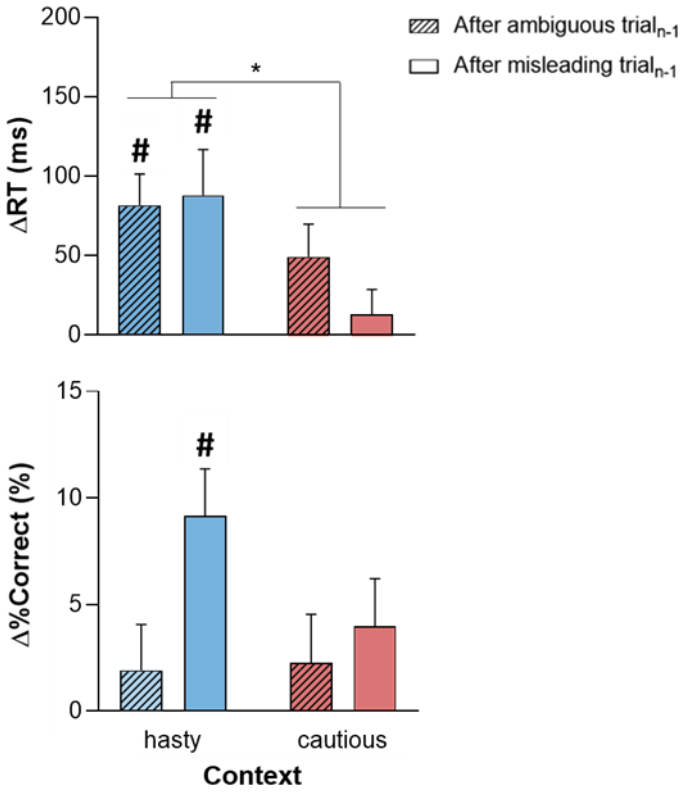

Figure 4: Post-error adjustments of reaction time (ΔRT; upper panel) and %Correct (Δ%Correct; lower panel) depending on the context (hasty or cautious) and on whether $trial_{n-1}$ was ambiguous (crosshatched bars) or misleading (empty bars). While the positive ΔRT in all conditions suggest the presence of PES, this slowing down was only significant in the hasty context. The latter PES came with a positive Δ%Correct but this effect was only significant following misleading $trials_{n-1}$. Error bars represent SE. #: t-test against 0 (significant difference from 0). *p < .05: significantly different.

In conclusion, our data indicate that post-error adjustments varied according to the context in which subjects performed the Tokens task, with PES being only significant in the hasty context, and a gain in performance being only observed after errors in misleading trials.

	FACTOR	t-value	p-value	Cohen's *d*	BF_{10}
ΔRT	after ambiguous $trials_{n-1}$ in hasty context	4.131	**< .001**	.767	98.677
	after misleading $trials_{n-1}$ in hasty context	3.053	**.005**	.567	8.330
	after ambiguous $trials_{n-1}$ in cautious context	2.390	.024	.444	2.207
	after misleading $trials_{n-1}$ in cautious context	.853	.401	.158	.275
Δ%Correct	after ambiguous $trials_{n-1}$ in hasty context	.894	.379	.166	.284
	after misleading $trials_{n-1}$ in hasty context	4.208	**< .001**	.781	118.923
	after ambiguous $trials_{n-1}$ in cautious context	.994	.329	.185	.310
	after misleading $trials_{n-1}$ in cautious context	1.772	.087	.329	.786

Table 3. Inferential Student's t-tests of behavioral changes in $trial_n$. The critical t-value, the p-value and the Cohen's *d* as a measure of the effect size are represented for each factor (after ambiguous or misleading $trials_{n-1}$ in hasty or cautious context), following the analysis of reaction time and %Correct change in $trial_n$ (ΔRT and Δ%Correct). Significant p-value (with a Bonferroni-corrected threshold of .05/4) are highlighted in bold and blue.

4.4. Discussion

The literature on post-error adjustments is quite diverse and controversial, especially regarding the nature of PES; although often adaptive, PES sometimes comes with a decline in accuracy, suggesting that it can be maladaptive in some instances. Here, we investigated if the nature of PES can vary according to whether a subject behaves in a context favoring hasty or cautious decisions. To address this point, we had subjects perform the Tokens task in separate blocks where errors were either poorly penalized, encouraging hasty responses (but low accuracy), or highly penalized, calling for more cautiousness (at the cost of speed). The results show that, overall, subjects slowed down after erroneous choices, supporting the presence of PES. Yet, despite the fact that ΔRT values

were numerically positive in all conditions, this PES was only significant in the hasty context (after correction for multiple comparisons). Moreover, consistent with an adaptive adjustment in this context, we observed a significant improvement in performance, but only following misleading trials$_{n-1}$; the positive ∆%Correct did not reach significance following ambiguous trials$_{n-1}$.

The positive values of ∆RT in all conditions indicate that, if anything, subjects slowed down after an error. However, contrary to our expectation to observe PES in the two contexts, this ∆RT was only significant in the hasty context suggesting that subjects only slowed down when they were in a context emphasizing speed (low accuracy) but not when the context promoted more accurate choices. PES, as observed in the hasty context, is usually associated with a cognitive control process recruited to prevent future errors (Beatty et al., 2020; Siegert et al., 2014; Smith & Brewer, 1995). Such process is thought to operate at least in part at the level of the decision threshold, increasing its height with respect to baseline activity as a means to augment the amount of (neural) evidence accumulation required to reach the decision threshold (Alamia et al., 2019; Derosiere et al., 2019, 2022; Dutilh et al., 2012; Fischer et al., 2018; Derosiere et al., 2018; Purcell & Kiani, 2016; Schiffler et al., 2017); this of course prolongs the decision time but increases the probability of choosing the right circle and therefore the reward rate.

Consistent with the occurrence of such adaptive adjustment maximizing the reward rate in the hasty context, the PES observed there was associated with positive ∆%Correct values (Botvinick & Braver, 2015; Vassiliadis & Derosiere, 2020; Thura, 2020). Yet surprisingly, this was only true after misleading trial$_{n-1}$ but not after ambiguous trial$_{n-1}$, as ∆%Correct did not reach significance following

the latter trial type. Hence, PES in the hasty context led to a gain in performance following misleading $trial_{n-1}$ but not after ambiguous $trial_{n-1}$. Such a finding suggests that errors did not solely trigger shifts in decision thresholds. Indeed, if this had been the case, one would have expected PES to be accompanied by a consistent increase in accuracy regardless of the type of $trial_{n-1}$ in which an error occurred. Alternatively, a non-exclusive possibility is that task engagement varied following errors in these two $trial_{n-1}$ types. We believe this may be the case because post-error task engagement (or arousal) has been shown to vary with the level of confidence at the moment an error is made (Desender et al., 2019; Purcell & Kiani, 2016; Yeung & Summerfield, 2012), which itself depends on the amount of sensory evidence available to make the (incorrect) choice (Desender et al., 2019; Meyniel et al., 2015; Pouget et al., 2016; Sanders et al., 2016; Urai et al., 2017). Accordingly, past studies have shown that when errors are made based on poor sensory evidence (i.e., with a low confidence level, as in ambiguous trials), arousal decreases significantly in the following trial (Navarro-Cebrian et al., 2013; Castellar et al., 2010; Desender et al., 2019; Notebaert et al., 2009; Purcell & Kiani, 2016; Wessel, 2018), possibly precluding an initially adaptive PES from leading to a significant gain in performance. By contrast, as previously observed in cognitive interference tasks, when errors are related to the presence of high (conflicting) sensory evidence (as in misleading trials), arousal is found increased in the following trial, an effect that may help dedicate attention to relevant sensory evidence (Danielmeier et al., 2011; King et al., 2010). Hence, it is plausible that in the current study, post-error task engagement was larger following misleading than ambiguous $trial_{n-1}$, allowing PES to result in a performance gain following the former but not the latter trial type. Such a hypothesis could be tested in future work by investigating

changes in pupil diameter following errors in our task (Kahneman & Beatty, 1966; Saderi et al., 2021).

Critically, Wessel proposed that PES arise from a sequence of processes including first a transient automatic response to the unexpected event (i.e., error), which triggers a reorientation of attention, followed by an adaptive process increasing decision threshold to prevent future errors (Wessel, 2018). Based on this adaptive orienting theory, the delay between the feedback on $trial_{n-1}$ (indicating an error) and the start of $trial_n$, which corresponds to the intertrial interval (ITI) duration, can influence the nature of PES and needs to be long enough to allow the second adaptive process to take place. This was the case in our study where the ITI duration was 2500 ms which, based on Wessel, is long enough for the adaptive process to occur. Hence, because the ITI duration was also comparable between the PES conditions, it is unlikely that this aspect of the task affected our data.

Unexpectedly, in this study we observed PES only in the hasty but not in the cautious context. One tempting explanation is that slowing down after errors could only effectively increase accuracy in the hasty but not in the cautious context. That is, because subjects emphasized speed in the hasty context, it is likely that a great proportion of errors were made because subjects responded too fast and not necessarily because the trial was difficult (Damaso et al., 2020). Hence, in this context, errors could easily be avoided by slowing down a bit in the following trial. In contrast, subjects were generally more cautious in the other context and it is thus plausible that errors occurred when choices were complex rather than because responses were too hasty (Brown & Heathcote, 2008; Ratcliff & McKoon, 2008; Ratcliff & Rouder, 1998). Slowing down following these trials may not

be effective as it would not necessarily enhance accuracy; that is, even if subjects fail on the most complex choices, they are generally cautious enough to succeed on most trials and slowing down further would not lead to any performance gain. Yet, we believe such an explanation does not hold here. As such, it is important to note that RTs in cautious blocks were around 2017 ms, which falls between $Jump_{10}$ and $Jump_{11}$, coinciding thus with the moment sensory evidence in favor of the correct choice starts to increase greatly (see methods). This means that even if subjects were already generally cautious (and slower) in this context, slowing down would have been adaptive because it would have allowed to provide responses based on more evidence.

A more plausible explanation is that the absence of PES in the cautious context is related to the way we promoted cautiousness in the current study. As such, changes in the SAT policy between the two contexts were engendered by manipulating the penalty size. However, even if error punishment is known to increase cautiousness (Derosiere et al., 2022; Potts, 2011), as desired here, monetary losses also generate an emotional response (Carver, 2006; Eben et al., 2020a; Frijda et al., 2014; Simões-Franklin et al., 2010), a sense of frustration increasing with the size of the loss (Eben et al., 2020c; Gehring & Willoughby, 2002; Holroyd et al., 2004;Yeung & Sanfey, 2004). Importantly, such negative emotion has been shown to induce a post-error acceleration of RTs rather than a slowdown (Damaso et al., 2020; Dyson, 2021; Dyson et al., 2018; Eben et al., 2020; Verbruggen et al., 2017). Accordingly, several studies have found that subjects act more impulsively after a loss or a nonrewarded trial than a rewarded one (Eben et al., 2020c; Gipson et al., 2012; Verbruggen et al., 2017). Altogether, this literature suggests that the emotional response to monetary loss might have precluded us from observing PES in the

cautious context. In other words, errors in the cautious context may have triggered opposite reactions counteracting each other; that is, a frustration feeling due to the high penalty (speeding up behavior) and an adaptive adjustment to prevent hasty errors (slowing down behavior). In the future, it would be interesting to dissociate the manipulation of the context from that of the penalty. Moreover, as the level of punishment sensitivity impacts error monitoring (Bradley et al., 2018; Unger et al., 2012), it also seems relevant to add some questionnaires to measure this personality trait such as the behavioral inhibition system (BIS) scale.

Interpretation of the current data is limited by the fact that a large number of subjects were excluded from the analyses because of an insufficient number of trials, reducing thus the sample size and the statistical power. In addition, the low error rate in the cautious context and the presence of different trial types impacted also the calculation of PES by preventing the use of another method than the traditional one. We recognize that this traditional method is prone to different biases such as global fluctuations in subject performance or in the number of post-correct trials outnumbering the number of post-error trials (Schroder et al., 2020). Note that even if some studies show that these biases can lead to an underestimation of post-error adjustments by decreasing effect sizes (Damaso et al., 2020; Schroder et al., 2020), others suggest that these biases do not radically change the results (Murphy et al., 2016b; van den Brink et al., 2014).

In conclusion, our findings highlight a complex combination of processes that come into play following errors and that affect the speed of ensuing actions as well as the degree to which such post-error adjustment comes with a gain in performance or is rather maladaptive. The recruitment of these processes depends on several

factors, including the context within which choices are made and the nature of erroneous trials, which affect altogether the subjects' strategy, their engagement in the task and likely also their emotional reaction to the error.

5. General discussion

During my PhD, I tried to better understand how urgency context influences motor behavior. This led me to realize two distinct studies: Chapter 1 investigated the impact of urgency on the interactions between decision making and movement execution, while Chapter 2 focused on its influence on post-error adjustments. Briefly, in Chapter 1, the findings reveal that under high urgency conditions, both decision and movement speeds are inherently accelerated. This acceleration occurs by default when it allows to maximize the reward rate, or at least, when it is not detrimental to it. These results are consistent with another study led by Thomas Carsten in our group and to which I contributed (Carsten et al., 2023). Moving on to Chapter 2, our research demonstrates that post-error adjustments are influenced by the urgency context. A slowdown is observed exclusively in a context of high urgency, occasionally accompanied by an increase in accuracy. Altogether, these results led me to some interesting observations that I will further discuss below and that are related to (1) the concept of maximization of reward rate; (2) the neural substrates of urgency; (3) the role of the arousal system and; (4) final considerations on the urgency signal.

5.1. Decision policy reflects the aim to optimize the reward rate.

In both studies, participants demonstrated adaptive decision making, finely tuning their decision speed to optimize rewards. More precisely, their decision policy reflected the search for a good balance between the caution to insure the choice correctness and the urgency to limit reward discounting. Heightening caution prolonged deliberation time, enhancing the likelihood of selecting actions yielding rewards. This phenomenon is particularly pronounced in the Tokens task,

where the probability of success increases throughout the trial (Cisek et al., 2009; Derosiere et al., 2022). However, it is crucial to note that extending deliberation time is associated with a decrease in the subjective value of the reward, a phenomenon known as "(temporal) reward discounting" (Berret & Baud-Bovy, 2022; Haith et al., 2012; Shadmehr et al., 2010). Combining these aspects, the evolution of the reward rate in a trial can be conceptualized as a function of deliberation time (Carland et al., 2019). More precisely, the reward rate increases over time in tandem with the rising success probability until the "additional" deliberation time becomes a waste of time compared to the improvement in accuracy. At this juncture, the reward rate function begins to decline. Therefore, the optimal decision duration is described as the moment when the reward rate is maximized.

In Chapter 1, the interaction between decision making and movement execution was contingent on the task goal. Specifically, we identified a default coregulation when it facilitated the maximization of reward rate, or at least when it did not compromise it. Chapter 2 revealed that post-error slowing in high urgency was accompanied by increased accuracy, particularly when errors occurred in misleading trials. However, despite the explanation of these results through the lens of reward maximization, several studies, including Heitz et al. (2014), highlight the suboptimal nature of human behavior. Humans often prioritize accuracy over time, evidenced by decision durations that exceed optimal durations for maximizing reward rate (Balci et al., 2011; Bogacz et al., 2006b, 2010; Maddox & Bohil, 2004). This suboptimal behavior could explain why we observed less evidence than expected for a coregulation between decision making and movement execution when we manipulated the movement speed in Experiment 2 of Chapter 1. As a reminder, in this experiment, although subjects in the fast decision group decided more quickly when they

had to perform fast movements, change in decision speed did not correlate with block-related change in movement speed. This discrepancy might be due to our experimental design, where the number of trials was fixed in both fast and slow movement blocks, limiting opportunities for getting the reward. Consequently, the urgency to respond was likely tempered in fast movement blocks to ensure decision accuracy, leading to a dissociation between the two levels of control. Furthermore, the absence of clear post-error speeding effect in the low urgency context of Chapter 2 could also be explained by an over-cautious behavior in our human subjects. Interestingly, such a post-error speeding was reported in non-human primates performing a similar task (Thura et al., 2017), possibly due to their more impulsive nature than humans (Boehm et al., 2016). Therefore, we hypothesized that errors in the low urgency context may have triggered opposite reactions counteracting each other; that is, a frustration feeling due to the high penalty associated with incorrect choices (which speeded up behavior) and an adaptive adjustment to prevent hasty errors (which slowed down behavior).

Nevertheless, as discussed in the preceding chapter, human behavior appears to be in a constant state of adaptation, suggesting that the tradeoff between decision caution and urgency can be refined with practice. The article by Thura (2020) supports this idea, revealing distinct behavioral adaptations between the two urgency contexts, particularly evident in the second session of their study. Hence, analyses of trial-to-trial and global behavior hinge on the subjects' understanding of task characteristics. As all the experiments began with a discovery block and some training, we can consider that the subjects had gone beyond the exploratory stage for the first experimental block. However, as explained in the previous paragraph, subjects seemed over-cautious in the Experiment 2 of Chapter 1 and

in the low urgency context of Chapter 2. The persistence of sub-optimal behavior implies that participants might not have fully learned the task characteristics when they performed the experimental blocks in my research. As a matter of course, we should observe an increased haste in making decisions once the task characteristics are learned. To test this hypothesis, we looked here at whether the order of the experiments had an impact on our results in the fast decision group of Experiment 2 (in Chapter 1). An additional mixed model analysis on decision durations (not reported in the Chapter) revealed a significant Block type X Experiment order interaction ($F_{1,9504.7}$= 11.034, $p < 0.001$, see Fig. 1). More specifically, the difference in decision duration between fast and slow movement blocks was only significant when subjects started with Experiment 1 (and thus performed Experiment 2 at a more advanced practice stage; $t_{1,9506.1} = 5.132$, $p < 0.001$) but not when they started the study with Experiment 2 ($t_{1,9503.1} = 0.591$, $p = 1.000$). A noteworthy model proposed by Doya in 1999 suggests that motor behavior at this stage integrates various learning types, including supervised and reinforced learnings (Doya, 1999; Fermin et al., 2016). This model posits a loop between the cerebellum, responsible for prediction, and the basal ganglia, focused on reinforcement. More precisely, the cerebellum would predict future behavioral outcomes (state), which are then evaluated by the prefrontal cortex and reinforced by the basal ganglia. Regardless of the context in which participants performed the Tokens task, they saw the last tokens jumps. These last token jumps were essential to understand the relevance of the feedback they got, especially for misleading trials. In this trial type, evidence at decision time often favored the selected circle (incorrect) before shifting to the correct one. Participants are likely to use the last token jumps to, at least partially, learn the characteristics of such a trial type. This supervised learning

not only facilitates adaptive behavior but also allows them to estimate the likelihood of selecting the correct circle on the first token jumps. This learning process may be further reinforced by rewarding feedback (points or monetary rewards in Chapters 1 and 2, respectively).

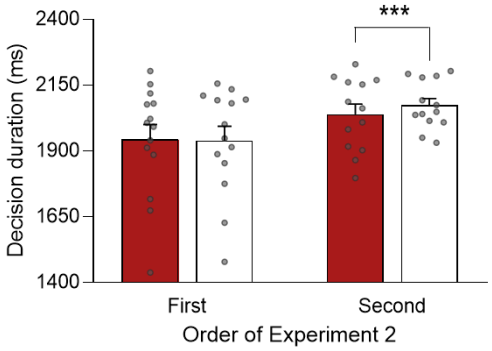

Figure 1. Decision duration in the fast decision group of Experiment 2 (Chapter 1). Data are separated depending on whether subjects performed this experiment first (before Experiment 1) or second (after Experiment 1). Note that the difference in decision duration between fast and slow movement blocks was only significant when subjects started with Experiment 1 (and thus performed Experiment 2 at a more advanced practice stage) but not when they started the study with Experiment 2. ***p < 0.001

To gain deeper insights into the potential for learning in the Token tasks and the ability to refine the balance between caution and haste towards optimized behavior, conducting experiments across multiple sessions would be valuable. Such an approach would enable the exploration of behavioral adaptations and shed light on the neural regions potentially involved in this intricate process.

5.2. Neural substrates shaping urgency

Our results in Chapter 1 suggest the operation of two different mechanisms: an invigoration mechanism controlling commonly decision and movement speed and a cognitive mechanism slowing down specifically the decision speed when it is required by the task

goal. Although these two mechanisms have already been discussed in the related paper, here, I am going to discuss their possible functioning and interaction more deeply.

In our Chapter 1, participants accelerated both their decision and movement speed under high urgency context, supporting the hypothesis of a common invigoration mechanism (Carsten et al., 2023; Thura, 2020; Thura et al., 2012, 2014). It has been suggested in the literature that such a mechanism might rely on an urgency signal generated from the Basal ganglia (Thura, 2020; Thura & Cisek, 2017). More precisely, Thura and Cisek (Thura & Cisek, 2017) found that the activity of Globus Pallidus around movement onset is modulated as a function of movement characteristics including the direction, speed and amplitude. This result is in line with the idea of basal ganglia being involved in the control of movement execution (Damier et al., 2007; Purves, 2001; Yttri & Dudman, 2018). In addition, correlations between striatal activity and threshold modulation have been observed in some studies, hinting at the involvement of striatal pathways in speed-accuracy tradeoffs at the decision making level (Forstmann et al., 2008a; Forstmann et al., 2010). To further explore such involvement, Thura & Cisek (2017) looked at pallidal cell activity during the deliberation phase. Their activity was weakly influenced by visual evidence, but appeared to be strongly influenced by the level of urgency within the block and the passage of time, suggesting a direct link between striatal pathways and the urgency signal. Moreover, while the urgency signal is described as a signal modulating the gain of sensory evidence (Cisek et al., 2009; Thura & Cisek, 2017), it is believed that basal ganglia amplifies motor gain (Park et al., 2020; Yttri & Dudman, 2018). More precisely, the striatum involves two pathways: a direct pathway releasing the tonic inhibition on the upper motor neurons in motor areas and an indirect pathway modulating the

disinhibitory actions of this direct pathway (Mosher et al., 2021; Purves, 2001). Hence, the excitability of both direct and indirect pathways would influence the signal-to-noise ratio in motor neural activity (Duque et al., 2017; Vassiliadis et al., 2020; Wilhelm et al., 2022; Yttri & Dudman, 2018). Increasing this ratio facilitates signal propagation (Greenhouse, 2022), expediting action selection by enhancing information flow from sensory areas. Simultaneously, it activates motor neurons and associated muscles, facilitating rapid execution while avoiding co-contractions (Bächinger et al., 2019; Mink, 1996; Shin et al., 2007). Such mechanism may be thus responsible for the surround inhibition, a phenomenon observed in studies applying transcranial magnetic stimulation (TMS) during movement preparation, which has traditionally been associated with an increase in movement vigor (Dudman & Krakauer, 2016; Shadmehr et al., 2019; Wilhelm et al., 2022) but which has also recently been linked to an increase in decision urgency (Derosiere et al., 2022).

In our Chapter 1, the clear coregulation between decision and movement in experiment 1 became less evident when we explored the inverse relationship by manipulating movement speed in Experiment 2. We did observe greater decision speed when subjects in the fast decision group performed fast movement blocks (compared to slow movement blocks). Yet, these changes in decision speed were not correlated to the block-related changes in movement speed. This lack of linear relationship could be attributed to subjects adopting a more cautious approach in this experiment, limiting the acceleration of decisions through the common invigoration mechanism. The use of a fixed number of trials instead of a fixed block duration constrained the potential for reward acquisition, prompting subjects to prioritize accuracy as well as speed (Heitz, 2014). The idea that a “caution mechanism” can break the coregulation between decision making and

movement execution is supported by the results obtained on participants of the slow decision group in the same experiment. Indeed, while the task design clearly favored choice accuracy in this group, block-related changes in movement speed did not impact decision making here. Furthermore, consistent with Thura's team's findings (Reynaud et al., 2020; Saleri Lunazzi et al., 2021), the inter-subject correlation between changes in decision and movement speed was negative. This implies that the emphasis on decision accuracy prompted this group to engage processes that maintained an appropriate level of accuracy despite the fact that switching from slow to fast movement blocks let to a joint invigoration of decision with movement speed. Hence, it is plausible that a cognitive control process intervenes, selectively shaping decision parameters in a goal-directed manner, effectively "holding the horses" in response to the invigoration originating from the instruction to move fast. Interestingly, some studies showed a close link between the activity of the hyperdirect pathway from medial frontal cortex to subthalamic nucleus (STN) and an increase in selection threshold (Aron et al., 2016; Herz et al., 2017; Pote et al., 2016). Critically, while a modulation of the selection threshold is mathematically equivalent to a decrease in the starting point (Churchland et al., 2008; Ditterich, 2006; O'Connell et al., 2018), upper motor neurons appear to systematically reach the same level of activity at the moment of action selection (Murphy et al., 2016a; Steinemann et al., 2018; Thura & Cisek, 2014). This suggests that the increase in the selection threshold by STN is actually induced by an inhibition of these neurons, resulting in a slowdown in decision making. In line with this idea, the hyperdirect pathway has been associated with a broad, non-specific inhibition in motor areas during conflict resolution and during action stopping (Aron et al., 2016; Duque et al., 2016; Klein et al., 2014; Frank et al., 2015; Mosher et al., 2021;

Neubert et al., 2010; Wessel et al., 2022). This effect would also be linked to a broad motor cortex suppression observed in past TMS studies, showing for instance reduced excitability in finger but also in leg muscles during cautious finger responses (Derosiere et al., 2022; Duque et al., 2017).

Hence, the duration of decision making may be shaped by the interplay of several processes, with two key influences highlighted in Chapter 1. On the one hand, a global invigoration process generated by striatal pathways may accelerate decisions along with accompanying movements. On the other hand, a cognitive control process, originating at the level of the hyperdirect pathway of the basal ganglia, may introduce caution into our decision making, leading to delays. However, given that the STN is involved in both circuits, a crucial question arises: how could the hyperdirect pathway possibly slow down decision speed without affecting movement speed? While this specific question has not been directly addressed, there is some evidence in the literature that supports this hypothesis. First, Mosher et al (2021) showed a fine anatomical and functional segregation between cells of the indirect and hyperdirect pathways. Second, patients with Parkinson's disease (PD) show greater difficulty than participants from the control group for inhibiting the initiation of action in stop signal task (Jahanshahi et al., 2015; Obeso et al., 2011a; Obeso et al., 2011b, see Hannah & Aron, 2021 for review). This result suggests a certain impulsivity in those patients (i.e., a lack of motor inhibition), which may seem counter-intuitive considering the motor slowing (bradykinesia) typical of PD. Interestingly, levodopa, which is a gold standard in the treatment of PD symptoms (LeWitt, 2015), does not improve motor inhibition in Parkinson's disease patients (Obeso et al., 2011b), which supports the idea of a dissociation between striatal and hyperdirect pathways. Nevertheless, despite their seemingly

distinct effects, we found a correlation with the UPPS score and changes in decision speed between fast and slow movements blocks in the slow decision group of Experiment 2. This implies a potential interaction between the two processes. While this correlation is only marginally significant, its presence suggests that individuals with higher impulsivity may struggle to decelerate their decision speed in fast movement blocks. In simpler terms, the invigoration mechanism might be associated with a specific impulse tied to the attraction for one action over another, and this impulse could be regulated by cognitive control. This observation holds significant implications, suggesting that motor impulsivity is not solely linked to an overactivity of striatal pathways but also stems from an underactivity of the hyperdirect tract. Consequently, only the interplay between these two processes, as observed in our study, could offer a more nuanced understanding of the deficiency in motor inhibition. This insight could potentially elucidate why previous studies failed to establish a correlation between impulsivity scores derived from questionnaires and movement speed (Reppert et al., 2015; Shadmehr et al., 2019).

In conclusion, shedding light on these two processes refines our comprehension of action control and the challenges associated with motor inhibition. Despite the substantial insights gained from our behavioral study, it is essential to acknowledge that the proposed hypothesis remains speculative due to the absence of physiological data. Further research endeavors incorporating physiological measurements and investigations within clinical populations would be invaluable. Such studies hold the potential to provide a more comprehensive understanding of these distinct processes and their potential interactions, contributing significantly to the advancement of our knowledge in the realm of action control and motor inhibition.

5.3. Role of the arousal system in decision making

In both chapters, the Tokens task placed a greater demand for precision on decision making compared to movement execution. Indeed, the movement was a flexion of an index finger that was either recorded by lasers (Chapter 1) or by a keyboard (Chapter 2), and therefore required little control in terms of accuracy. By contrast, decision making was more complicated since choice accuracy depended on token jumps (dynamic evidence). Therefore, most of attentional resources were probably directed toward processes controlling decisions. This could explain why, in our studies, subjects tended to prioritize accuracy at the expense of time, as discussed earlier. Moreover, this could account for the increase in pupil dilation in the fast and slow decision blocks in the Experiment 1 of Chapter 1, indicating the recruitment of the arousal by both the global invigoration and the cognitive control processes.

The increase in arousal in a high urgency context has been reported in several past studies (Gross & Dobbins, 2021; Murphy et al., 2016a; Reppert et al., 2015, 2023; Steinemann et al., 2018; Thura et al., 2014). Consistently, these studies showed that pupil is more dilated when subjects have to make fast decisions compared to slow ones (Gross & Dobbins, 2021; Murphy et al., 2016a; Reppert et al., 2023; Steinemann et al., 2018). Although the pupil size in our Chapter 1 was not influenced by the type of block, we observed a positive correlation between the urgency signal and pupil dilation, indicating that higher urgency levels are associated with greater pupil dilation. Notably, increased pupil dilation has been linked to improved encoding of sensory evidence in the visual cortex (Steinemann et al., 2018), suggesting a key role for the arousal system in facilitating the influx of sensory information. Furthermore, there is evidence of increased saccade vigor in urgent contexts (Reppert et al., 2015; Thura et al.,

2014), indicating a propensity for information seeking (Gottlieb et al., 2014). Critically, in our Chapter 1, we interpreted the recruitment of the arousal system as an increase in sensory information gain at the decision level due to the increase in urgency in fast decision blocks. However, the role of such a recruitment remains unclear. Steinemann et al. (2018) suggested that it could reflect an increase in attention, enhancing information processing at the sensory level to limit the decrease in accuracy. Alternatively, it could simply be a phenomenon enabling subjects to be more sensitive at the decision level to the evidence present in the environment. In the first case, subjects would be performing better, shifting their speed-accuracy tradeoff (SAT) curve to the left (i.e., having higher accuracy for a same decision duration). In the second case, they would be changing their response strategy, sliding along their SAT curve to the left (i.e., making faster decisions at the expense of accuracy). Interestingly, the inverse efficiency score (IES) was significantly lower in fast decision blocks compared to slow decision blocks (20 ± 2.58 and 23.81 ± 1.11, respectively, $t_{1,55} = -10.725$, $p < 0.001$, Cohen's $d = -1.433$). The IES, defined as the mean decision duration of correct choices divided by the percentage of correct choices (Liesefeld & Janczyk, 2019), indicated higher performance in fast decision blocks. While consistent with Steinemann's interpretation, it is important to note that the calculation of the IES might be influenced by our task design, which involved, here, different proportion of three trial types with evidence changing over time. In the future, it would be interesting to conduct similar analyses in a task with fewer biases related to trials (e.g., a task with one type of trial where the level of evidence is constant over time). Such a task would help to clarify the effect of pupillary dilation on the SAT curve.

The strategic recruitment of arousal to favor caution is less studied in the literature, but our findings in the different chapters provide some evidence in this direction. In Chapter 1, we found a greater pupil dilation in slow decision blocks relative to fast ones in ambiguous trials with the same decision duration. Moreover, the increase in pupil dilation in ambiguous trials of slow decision blocks was correlated with an increase in percentage of correct choices in this context suggesting strategic allocation of resources to promote accuracy. Although we did not measure pupil size in Chapter 2, the post-error slowing observed in the high urgency context went sometimes along with an increase in accuracy. This result also implies that the cognitive control mechanism can recruit attentional resources to improve the subject's performance. This aligns with some studies suggesting a connection between the hyperdirect pathway of the basal ganglia and the locus coeruleus (Wessel, 2018; Xu et al., 2022). Specifically, Wessel's model proposed that the activation of the hyperdirect pathway facilitates the orientation of attention toward sensory information relevant to the task (Wessel, 2018). Xu et al. demonstrated that the activity of both the STN and the locus coeruleus correlates with the ability to slow down after the onset of a stop signal, indicating better capacity to cancel a motor command and likely better detection of the stopping signal as well (Xu et al., 2022). Critically, it is noteworthy that the post-error slowing observed in Chapter 2 was not always accompanied by an increase in accuracy. Indeed, the post-error slowing led to an increase in accuracy when the error was made in a misleading $trial_{n-1}$ only (there were no change in accuracy when the error was made in an ambiguous $trial_{n-1}$). The result might be linked to the characteristic of the misleading trials. As a reminder, in these trials the tokens initially jump in the wrong circle before switching and jumping mainly in the correct one. The SumLogLR was positive at the

reaction time in misleading trial$_{n-1}$, suggesting that subjects made their error when the evidence was still favoring the wrong circle. Therefore, the discrepancy between the evidence at the decision time (favoring the wrong circle) and the evidence at the end of the trial (favoring the correct circle) plays a crucial role in driving the subject's attention. Moreover, as post-error adjustments were exclusively measured in ambiguous trial$_n$, the recruitment of the arousal system did not seem impacted by the immediate improvement possibility within the ambiguous trial$_n$ but rather by the potential for enhancement in the previous misleading trial$_{n-1}$. This nuanced understanding of how the locus coeruleus responds to specific error types and the temporal dynamics of improvement possibilities adds depth to our comprehension of the neural mechanisms underlying adaptive decision making. It also underscores the complexity of the interplay between attentional processes and performance optimization in cognitive tasks. However, whether in our study or in the literature, the link between the arousal system and decision accuracy is only indirectly observed. In order to better understand the role of the arousal system in decision making, it is important to study its direct involvement in a causal manner by using stimulation techniques such as transcutaneous vagus nerve stimulation (Hilz, 2022).

5. 4. Computation of the urgency signal

My PhD project focused on understanding behavioral adaptations under urgency contexts, with a central concept being the urgency signal. This signal is derived from the distribution of decision durations and serves as a reflection of how participants adapt their decision policy to various task contexts. In Chapter 2, we faced data limitations, preventing us from modeling the urgency signal. Therefore, this section will concentrate on the results from Chapter 1. Sometimes

correlated with the movement speed sometimes not, this signal seems a faithful reflection of the different processes shaping decision speed, encompassing both the common invigoration and eventual cognitive mechanisms coming into play to optimize reward rate. More precisely, we found a correlation when context-dependent changes in decision speed led to clear changes in movement speed (Experiment 1). In fast decision blocks, where decision accuracy was less critical due to the opportunity provided by additional trials, the invigoration mechanism dominated over caution. Conversely, in slow decision blocks, where subjects prioritized accuracy, as discussed in the previous section (see the section 5.3. Role of arousal system in decision making), the cognitive mechanism likely took precedence over invigoration. This clear switch between predominant mechanisms might explain why a correlation between decisional urgency and movement speed was evident in this experiment. In Experiment 2, subjects appeared to prioritize both speed and accuracy, making the shift between the two mechanisms less obvious. The design of the study, limiting the possibility of obtaining rewards irrespective of block conditions, may contribute to this observation. So, even if the invigoration mechanism is activated by the execution of fast movement (in fast movement blocks), its effect could be diminished by the cognitive mechanism, ensuring a minimum of precision. As the last mechanism seems specific to decision making (see section 5.2. Neural substrates shaping urgency), its recruitment, in parallel with the recruitment of the common invigoration mechanism, may explain the lack of correlation between decisional urgency and movement speed in this experiment.

It is noteworthy that, according to the literature, the urgency signal can be computed in various forms. While a linear function is the most common, some authors have explored alternatives such as polynomial functions (Derosiere et al., 2022; Murphy et al., 2016a; Standage et

al., 2011; Steinemann et al., 2018; Thura & Cisek, 2017). Interestingly, despite the differences in shape, these forms tend to work in similar ways. One contributing factor is the application of signal rectification, particularly when the signal is negative (the result of a negative intercept). This notion gained support through an additional analysis in Experiment 1. We compared the mean square error between data distributions of the model and actual data distributions (k-distance) across four models (not reported in the Chapter 1), each employing a different computation of the urgency signal: a linear urgency with a constant intercept set at 0, a rectified linear urgency with a negative intercept, a polynomial urgency, and an exponential urgency. To ensure equitable comparison between the linear urgency models, we measured the maximum distance between the intercept and the selection threshold in the rectified linear model (3.52) and sought the best fit with a threshold range between 1 and 4 for each subject in the urgency model with an intercept set to 0. On average, the k-distance was 0.167 ± 0.069 for the linear urgency model, 0.063 ± 0.014 for the rectified linear urgency model, 0.067 ± 0.018 for the exponential urgency model, and 0.076 ± 0.028 for the polynomial urgency model. Bayesian paired t-tests revealed that only the models with rectified linear and exponential urgency demonstrated an equivalent fit, displaying a lower k-distance than the other two models (see Table 1). While statistical tests indicated a significant difference between these two models and the polynomial one, the minimal difference in k-distance (0.011 ± 0.026) suggests that these three models are, in practice, equivalent.

Model comparison	BF_{10}	error%
linear urgency vs rectified linear urgency	**5.177×10^{12}**	**1.936×10^{-15}**
linear urgency vs exponential urgency	**1.847×10^{12}**	**2.115×10^{-14}**
linear urgency vs polynomial urgency	**3.266×10^{9}**	**7.827×10^{-16}**
rectified linear urgency vs exponential urgency	0.529	0.036
rectified linear urgency vs polynomial urgency	**90.272**	**8.800×10^{-9}**
exponential urgency vs polynomial urgency	**3.785**	**6.281×10^{-7}**

Table 1. Comparison of the fit between four versions of the urgency gating models. The table compares the ability to reproduce the real data distribution of the four urgency gating models with Bayesian paired t-tests on their mean square-error between data distributions of the model and the real data distributions. BF_{10} grades the strength of evidence for the alternative hypothesis against the null hypothesis. The error percentage (Error %) indicates the numeric robustness of the results, with low values of the Error % corresponding to a greater numerical stability of results. Significant differences are highlighted in bold and blue.

While the k-distance analysis suggests comparable fitting abilities among models employing a rectified linear urgency signal, an exponential signal, and a polynomial one, we maintain that the rectified linear model distinctly captures the diverse mechanisms at play in decision making. Specifically, we can associate, to a certain degree, the parameters of the urgency signal (intercept and slope) with the invigoration and cognitive mechanisms. More precisely, the common invigoration mechanism is recognized for robustly elevating urgency right from the beginning of the deliberation phase, progressively intensifying over time (Cisek et al., 2009; Thura, 2020; Thura et al., 2014). In contrast, the cognitive mechanism notably diminishes urgency levels at the onset of the deliberation phase, gradually reducing its impact to allow action selection. Therefore, a higher intercept signifies a greater predominance of invigoration, while a lower intercept, approaching negative values, indicates a greater predominance of caution. The urgency slope reflects the acceleration of decision making over time, a phenomenon influenced, at least in

part, by the temporal dynamics of the invigoration mechanism. To test this hypothesis, exploring how physiological data related to each mechanism correlates with the urgency signal parameters would be insightful. Such an investigation could provide a nuanced understanding of the distinct mechanisms influencing decision making.

6. General conclusion

In summary, our findings revealed a nuanced interplay among various mechanisms influencing both decision making and movement execution. Chapter 1 brought forth two key mechanisms: a common invigoration mechanism responsible for a natural coregulation between decision and movement speed, and a likely cognitive mechanism, decelerating decisions when the common invigoration mechanism is active but reward is tied to choice accuracy. Intriguingly, these mechanisms demonstrated a close relationship with the arousal system, evidenced by increased pupil dilation in both high and low urgency contexts. Chapter 2 underscored the prominence of the cognitive mechanism, with a post-error slowing in high urgency context. Notably, it proposed that the arousal system was solicited by this mechanism solely when there is a discrepancy between the evidence at the decision time and the evidence at the end of the trial.

Consequently, both studies unveiled a consistent theme: behavioral adaptations align with a singular rule; to optimize the rate of reward. However, these observations prompt several intriguing questions: How effectively can we optimize our behavior? To what extent does the interplay between the common invigoration process and the cognitive process contribute to a refined understanding of impulsivity? What is the true involvement of the arousal system in decision making and to what degree does its recruitment by different processes signify distinct mechanisms? How does a comprehensive representation of the urgency signal aid in identifying the diverse mechanisms at play in decision making? These questions provide a fertile ground for further investigations, offering potential avenues to deepen our understanding of the intricate dynamics shaping human behavior in response to urgency.

7. References

Alamia, A., Zénon, A., VanRullen, R., Duque, J., & Derosiere, G. (2019). Implicit visual cues tune oscillatory motor activity during decision-making. *NeuroImage*, *186*, 424-436. https://doi.org/10.1016/j.neuroimage.2018.11.027

Arnold, N. R., Bröder, A., & Bayen, U. J. (2015). Empirical validation of the diffusion model for recognition memory and a comparison of parameter-estimation methods. *Psychological Research*, *79*(5), 882-898. https://doi.org/10.1007/s00426-014-0608-y

Aron, A. R., Herz, D. M., Brown, P., Forstmann, B. U., & Zaghloul, K. (2016). Frontosubthalamic Circuits for Control of Action and Cognition. *The Journal of Neuroscience*, *36*(45), 11489-11495. https://doi.org/10.1523/JNEUROSCI.2348-16.2016

Audley, R. J., & Pike, A. R. (1965). SOME ALTERNATIVE STOCHASTIC MODELS OF CHOICE [1]. *British Journal of Mathematical and Statistical Psychology*, *18*(2), 207-225. https://doi.org/10.1111/j.2044-8317.1965.tb00342.x

Bächinger, M., Lehner, R., Thomas, F., Hanimann, S., Balsters, J., & Wenderoth, N. (2019). Human motor fatigability as evoked by repetitive movements results from a gradual breakdown of surround inhibition. *eLife*, *8*, e46750. https://doi.org/10.7554/eLife.46750

Balci, F., Simen, P., Niyogi, R., Saxe, A., Hughes, J. A., Holmes, P., & Cohen, J. D. (2011). Acquisition of decision making criteria : Reward rate ultimately beats accuracy. *Attention, Perception, & Psychophysics*, *73*(2), 640-657. https://doi.org/10.3758/s13414-010-0049-7

Barendregt, N. W., Gold, J. I., Josić, K., & Kilpatrick, Z. P. (2022). Normative decision rules in changing environments. *eLife*, *11*, e79824. https://doi.org/10.7554/eLife.79824

Beatty, P. J., Buzzell, G. A., Roberts, D. M., & McDonald, C. G. (2020). Contrasting time and frequency domains : ERN and induced theta oscillations differentially predict post-error behavior. *Cognitive, Affective, & Behavioral Neuroscience*, *20*(3), 636-647. https://doi.org/10.3758/s13415-020-00792-7

Berkay, D., Eser, H. Y., Sack, A. T., Çakmak, Y. Ö., & Balcı, F. (2018). The modulatory role of pre-SMA in speed-accuracy tradeoff : A bi-directional TMS study. *Neuropsychologia*, *109*, 255-261. https://doi.org/10.1016/j.neuropsychologia.2017.12.031

Berret, B., & Baud-Bovy, G. (2022). Evidence for a cost of time in the invigoration of isometric reaching movements. *Journal of Neurophysiology*, *127*(3), 689-701. https://doi.org/10.1152/jn.00536.2021

Berridge, K. C., & Robinson, T. E. (2016). Liking, wanting, and the incentive-sensitization theory of addiction. *American Psychologist*, *71*(8), 670-679. https://doi.org/10.1037/amp0000059

Boehm, U., Hawkins, G. E., Brown, S., Van Rijn, H., & Wagenmakers, E.-J. (2016). Of monkeys and men : Impatience in perceptual decision-making. *Psychonomic Bulletin & Review*, *23*(3), 738-749. https://doi.org/10.3758/s13423-015-0958-5

Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006a). The physics of optimal decision making : A formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological Review*, *113*(4), 700-765. https://doi.org/10.1037/0033-295X.113.4.700

Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006b). The physics of optimal decision making : A formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological Review*, *113*(4), 700-765. https://doi.org/10.1037/0033-295X.113.4.700

Bogacz, R., Hu, P. T., Holmes, P. J., & Cohen, J. D. (2010). Do humans produce the speed–accuracy trade-off that maximizes reward rate? *Quarterly Journal of Experimental Psychology*, *63*(5), 863-891. https://doi.org/10.1080/17470210903091643

Botvinick, M., & Braver, T. (2015). Motivation and Cognitive Control : From Behavior to Neural Mechanism. *Annual Review of Psychology*, *66*(1), 83-113. https://doi.org/10.1146/annurev-psych-010814-015044

Bourgeois, A., Chelazzi, L., & Vuilleumier, P. (2016). Chapter 14—How motivation and reward learning modulate selective attention. In B. Studer & S. Knecht (Éds.), *Progress in Brain Research* (Vol. 229, p. 325-342). Elsevier. https://doi.org/10.1016/bs.pbr.2016.06.004

Bradley, E., Laurent, R., Phibbs, F., Tolleson, C., Turchan, M., Wylie, S. A., van Wouwe, N. C., & van den Wildenberg, W. (2018). Motivational Sensitivities Linked to Impulsive Motor Errors in Parkinson's Disease. *Journal of the International Neuropsychological Society*, *24*(2), 128-138. Cambridge Core. https://doi.org/10.1017/S1355617717000741

Brown, S. D., & Heathcote, A. (2008). The simplest complete model of choice response time : Linear ballistic accumulation. *Cognitive Psychology*, *57*(3), 153-178. https://doi.org/10.1016/j.cogpsych.2007.12.002

Brown, S., & Heathcote, A. (2005). A Ballistic Model of Choice Response Time. *Psychological Review*, *112*(1), 117-128. https://doi.org/10.1037/0033-295X.112.1.117

Carland, M. A., Marcos, E., Thura, D., & Cisek, P. (2016). Evidence against perfect integration of sensory information during perceptual decision

making. *Journal of Neurophysiology*, *115*(2), 915-930. https://doi.org/10.1152/jn.00264.2015

Carland, M. A., Thura, D., & Cisek, P. (2015). The urgency-gating model can explain the effects of early evidence. *Psychonomic Bulletin & Review*, *22*(6), 1830-1838. https://doi.org/10.3758/s13423-015-0851-2

Carland, M. A., Thura, D., & Cisek, P. (2019). The Urge to Decide and Act : Implications for Brain Function and Dysfunction. *The Neuroscientist*, *25*(5), 491-511. https://doi.org/10.1177/1073858419841553

Carsten, T., Fievez, F., & Duque, J. (2023). Movement characteristics impact decision-making and vice versa. *Scientific Reports*, *13*(1), 3281. https://doi.org/10.1038/s41598-023-30325-4

Carver, C. S. (2006). Approach, Avoidance, and the Self-Regulation of Affect and Action. *Motivation and Emotion*, *30*(2), 105-110. https://doi.org/10.1007/s11031-006-9044-7

Castellar, E. núñez, Kühn, S., Fias, W., & Notebaert, W. (2010). Outcome expectancy and not accuracy determines posterror slowing : ERP support. *Cognitive, Affective, & Behavioral Neuroscience*, *10*(2), 270-278. https://doi.org/10.3758/CABN.10.2.270

Cavanagh, J. F., Sanguinetti, J. L., Allen, J. J. B., Sherman, S. J., & Frank, M. J. (2014). The Subthalamic Nucleus Contributes to Post-error Slowing. *Journal of Cognitive Neuroscience*, *26*(11), 2637-2644. https://doi.org/10.1162/jocn_a_00659

Cavanagh, J. F., Wiecki, T. V., Cohen, M. X., Figueroa, C. M., Samanta, J., Sherman, S. J., & Frank, M. J. (2011). Subthalamic nucleus stimulation reverses mediofrontal influence over decision threshold. *Nature Neuroscience*, *14*(11), 1462-1467. https://doi.org/10.1038/nn.2925

Ceccarini, F., Guerra, S., Betti, S., Vergazzini, A., Sartori, L., & Castiello, U. (2019). Changes in corticospinal excitability associated with post-error slowing. *Cortex*, *120*, 92-100. https://doi.org/10.1016/j.cortex.2019.05.015

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129-136. https://doi.org/10.1016/0040-5809(76)90040-X

Chen, X., & Yang, T. (2021). A neural network model of basal ganglia's decision-making circuitry. *Cognitive Neurodynamics*, *15*(1), 17-26. https://doi.org/10.1007/s11571-020-09609-2

Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed–accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution*, *24*(7), 400-407. https://doi.org/10.1016/j.tree.2009.02.010

Churchland, A. K., Kiani, R., & Shadlen, M. N. (2008). Decision-making with multiple alternatives. *Nature Neuroscience*, *11*(6), 693-702. https://doi.org/10.1038/nn.2123

Cisek, P. (2006). Integrated Neural Processes for Defining Potential Actions and Deciding between Them : A Computational Model. *The Journal of Neuroscience*, *26*(38), 9761-9770. https://doi.org/10.1523/JNEUROSCI.5605-05.2006

Cisek, P., Puskas, G. A., & El-Murr, S. (2009). Decisions in Changing Conditions : The Urgency-Gating Model. *The Journal of Neuroscience*, *29*(37), 11560-11571. https://doi.org/10.1523/JNEUROSCI.1844-09.2009

Cisek, P., & Thura, D. (2022). Models of Decision-Making Over Time. In P. Cisek & D. Thura, *Oxford Research Encyclopedia of Neuroscience*. Oxford University Press. https://doi.org/10.1093/acrefore/9780190264086.013.346

Coddington, L. T., & Dudman, J. T. (2019). Learning from Action : Reconsidering Movement Signaling in Midbrain Dopamine Neuron Activity. *Neuron*, *104*(1), 63-77. https://doi.org/10.1016/j.neuron.2019.08.036

Compton, R. J., Gearinger, D., Wild, H., Rette, D., Heaton, E. C., Histon, S., Thiel, P., & Jaskir, M. (2021). Simultaneous EEG and pupillary evidence for post-error arousal during a speeded performance task. *European Journal of Neuroscience*, *53*(2), 543-555. https://doi.org/10.1111/ejn.14947

Damaso, K., Williams, P., & Heathcote, A. (2020). Evidence for different types of errors being associated with different types of post-error changes. *Psychonomic Bulletin & Review*, *27*(3), 435-440. https://doi.org/10.3758/s13423-019-01675-w

Damier, P., Thobois, S., Witjas, T., Cuny, E., Derost, P., Raoul, S., Mertens, P., Peragut, J.-C., Lemaire, J.-J., Burbaud, P., Nguyen, J.-M., Llorca, P.-M., Rascol, O., & =French Stimulation for Tardive Dyskinesia (STARDYS) Study Group. (2007). Bilateral deep brain stimulation of the globus pallidus to treat tardive dyskinesia. *Arch Gen Psychiatry*, *64*(2), 170-176. PubMed. https://doi.org/10.1001/archpsyc.64.2.170

Danielmeier, C., Eichele, T., Forstmann, B. U., Tittgemeyer, M., & Ullsperger, M. (2011). Posterior Medial Frontal Cortex Activity Predicts Post-Error Adaptations in Task-Related Visual and Motor Areas. *The Journal of Neuroscience*, *31*(5), 1780. https://doi.org/10.1523/JNEUROSCI.4299-10.2011

Danion, F., Duarte, M., & Grosjean, M. (1999). Fitts' law in human standing : The effect of scaling. *Neuroscience Letters*, *277*(2), 131-133. https://doi.org/10.1016/S0304-3940(99)00842-3

Derosiere, G., Klein, P.- A., Nozaradan, S., Zénon, A., Mouraux, A., & Duque, J. (2018). Visuomotor Correlates of Conflict Expectation in the Context of Motor Decisions. *The Journal of Neuroscience*, *38*(44), 9486. https://doi.org/10.1523/JNEUROSCI.0623-18.2018

Derosiere, G., Thura, D., Cisek, P., & Duque, J. (2019). Motor cortex disruption delays motor processes but not deliberation about action choices. *Journal of Neurophysiology*, *122*(4), 1566-1577. https://doi.org/10.1152/jn.00163.2019

Derosiere, G., Thura, D., Cisek, P., & Duque, J. (2021). Trading accuracy for speed over the course of a decision. *Journal of Neurophysiology*, *126*(2), 361-372. https://doi.org/10.1152/jn.00038.2021

Derosiere, G., Thura, D., Cisek, P., & Duque, J. (2022). Hasty sensorimotor decisions rely on an overlap of broad and selective changes in motor activity. *PLOS Biology*, *20*(4), e3001598. https://doi.org/10.1371/journal.pbio.3001598

Desender, K., Boldt, A., Verguts, T., & Donner, T. H. (2019). Confidence predicts speed-accuracy tradeoff for subsequent decisions. *eLife*, *8*, e43499. https://doi.org/10.7554/eLife.43499

Desmurget, M., & Turner, R. S. (2010). Motor Sequences and the Basal Ganglia : Kinematics, Not Habits. *The Journal of Neuroscience*, *30*(22), 7685. https://doi.org/10.1523/JNEUROSCI.0163-10.2010

Diederich, A. (2003). MDFT account of decision making under time pressure. *Psychonomic Bulletin & Review*, *10*(1), 157-166. https://doi.org/10.3758/BF03196480

Ditterich, J. (2006). Evidence for time-variant decision making. *European Journal of Neuroscience*, *24*(12), 3628-3641. https://doi.org/10.1111/j.1460-9568.2006.05221.x

Doya, K. (1999). What are the computations of the cerebellum, the basal ganglia and the cerebral cortex? *Neural Networks*, *12*(7-8), 961-974. https://doi.org/10.1016/S0893-6080(99)00046-5

Drugowitsch, J., Moreno-Bote, R., Churchland, A. K., Shadlen, M. N., & Pouget, A. (2012). The Cost of Accumulating Evidence in Perceptual Decision Making. *The Journal of Neuroscience*, *32*(11), 3612-3628. https://doi.org/10.1523/JNEUROSCI.4010-11.2012

Dubravac, M., Roebers, C. M., & Meier, B. (2020). Different temporal dynamics after conflicts and errors in children and adults. *PLOS ONE*, *15*(8), e0238221. https://doi.org/10.1371/journal.pone.0238221

Dubravac, M., Roebers, C. M., & Meier, B. (2022). Age-related qualitative differences in post-error cognitive control adjustments. *British Journal of Developmental Psychology*, *40*(2), 287-305. https://doi.org/10.1111/bjdp.12403

Dudman, J. T., & Krakauer, J. W. (2016). The basal ganglia : From motor commands to the control of vigor. *Current Opinion in Neurobiology*, *37*, 158-166. https://doi.org/10.1016/j.conb.2016.02.005

Duque, J., Greenhouse, I., Labruna, L., & Ivry, R. B. (2017). Physiological Markers of Motor Inhibition during Human Behavior. *Trends in*

Neurosciences, *40*(4), 219-236. https://doi.org/10.1016/j.tins.2017.02.006

Duque, J., Petitjean, C., & Swinnen, S. P. (2016). Effect of Aging on Motor Inhibition during Action Preparation under Sensory Conflict. *Frontiers in Aging Neuroscience*, *8*. https://www.frontiersin.org/articles/10.3389/fnagi.2016.00322

Dutilh, G., Forstmann, B. U., Vandekerckhove, J., & Wagenmakers, E.-J. (2013). A diffusion model account of age differences in posterror slowing. *Psychology and Aging*, *28*(1), 64-76. https://doi.org/10.1037/a0029875

Dutilh, G., Vandekerckhove, J., Forstmann, B. U., Keuleers, E., Brysbaert, M., & Wagenmakers, E.-J. (2012). Testing theories of post-error slowing. *Attention, Perception, & Psychophysics*, *74*(2), 454-465. https://doi.org/10.3758/s13414-011-0243-2

Dyson, B. J. (2021). Variability in competitive decision-making speed and quality against exploiting and exploitative opponents. *Scientific Reports*, *11*(1), 2859. https://doi.org/10.1038/s41598-021-82269-2

Dyson, B. J., Sundvall, J., Forder, L., & Douglas, S. (2018). Failure generates impulsivity only when outcomes cannot be controlled. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(10), 1483.

Eben, C., Billieux, J., & Verbruggen, F. (2020a). Clarifying the Role of Negative Emotions in the Origin and Control of Impulsive Actions. *Psychologica Belgica*, *60*(1), 1-17. https://doi.org/10.5334/pb.502

Eben, C., Chen, Z., Cracco, E., Brass, M., Billieux, J., & Verbruggen, F. (2020b). Are post-error adjustments influenced by beliefs in free will ? A failure to replicate Rigoni, Wilquin, Brass and Burle, 2013. *Royal Society Open Science*, *7*(11), 200664. https://doi.org/10.1098/rsos.200664

Eben, C., Chen, Z., Vermeylen, L., Billieux, J., & Verbruggen, F. (2020c). A direct and conceptual replication of post-loss speeding when gambling. *Royal Society Open Science*, *7*(5), 200090. https://doi.org/10.1098/rsos.200090

Evans, N. J., Hawkins, G. E., Boehm, U., Wagenmakers, E.-J., & Brown, S. D. (2017). The computations that support simple decision-making : A comparison between the diffusion and urgency-gating models. *Scientific Reports*, *7*(1), 16433. https://doi.org/10.1038/s41598-017-16694-7

Evans, N. J., Hawkins, G. E., & Brown, S. D. (2020). The role of passing time in decision-making. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *46*(2), 316-326. https://doi.org/10.1037/xlm0000725

Fermin, A. S. R., Yoshida, T., Yoshimoto, J., Ito, M., Tanaka, S. C., & Doya, K. (2016). Model-based action planning involves cortico-cerebellar and basal ganglia networks. *Scientific Reports*, *6*(1), 31378. https://doi.org/10.1038/srep31378

Ferrucci, L., Genovesio, A., & Marcos, E. (2021). The importance of urgency in decision making based on dynamic information. *PLOS Computational Biology*, *17*(10), e1009455. https://doi.org/10.1371/journal.pcbi.1009455

Fievez, F., Derosiere, G., Verbruggen, F., & Duque, J. (2022). Post-error Slowing Reflects the Joint Impact of Adaptive and Maladaptive Processes During Decision Making. *Frontiers in Human Neuroscience*, *16*, 864590. https://doi.org/10.3389/fnhum.2022.864590

Fischer, A. G., Nigbur, R., Klein, T. A., Danielmeier, C., & Ullsperger, M. (2018). Cortical beta power reflects decision dynamics and uncovers multiple facets of post-error adaptation. *Nature Communications*, *9*(1), 5038. https://doi.org/10.1038/s41467-018-07456-8

Forstmann, B. U., Anwander, A., Schäfer, A., Neumann, J., Brown, S., Wagenmakers, E.-J., Bogacz, R., & Turner, R. (2010). Cortico-striatal connections predict control over speed and accuracy in perceptual decision making. *Proceedings of the National Academy of Sciences*, *107*(36), 15916-15920.

Forstmann, B. U., Dutilh, G., Brown, S., Neumann, J., Von Cramon, D. Y., Ridderinkhof, K. R., & Wagenmakers, E.-J. (2008a). Striatum and pre-SMA facilitate decision-making under time pressure. *Proceedings of the National Academy of Sciences*, *105*(45), 17538-17542.

Forstmann, B. U., Ratcliff, R., & Wagenmakers, E.-J. (2016). Sequential Sampling Models in Cognitive Neuroscience : Advantages, Applications, and Extensions. *Annual Review of Psychology*, *67*(1), 641-666. https://doi.org/10.1146/annurev-psych-122414-033645

Forstmann, B. U., van den Wildenberg, W. P. M., & Ridderinkhof, K. R. (2008b). Neural Mechanisms, Temporal Dynamics, and Individual Differences in Interference Control. *Journal of Cognitive Neuroscience*, *20*(10), 1854-1865. https://doi.org/10.1162/jocn.2008.20122

Frank, M. J., Gagne, C., Nyhus, E., Masters, S., Wiecki, T. V., Cavanagh, J. F., & Badre, D. (2015). fMRI and EEG Predictors of Dynamic Decision Parameters during Human Reinforcement Learning. *The Journal of Neuroscience*, *35*(2), 485. https://doi.org/10.1523/JNEUROSCI.2036-14.2015

Frank, M. J., Samanta, J., Moustafa, A. A., & Sherman, S. J. (2007). Hold Your Horses : Impulsivity, Deep Brain Stimulation, and Medication in Parkinsonism. *Science*, *318*(5854), 1309-1312. https://doi.org/10.1126/science.1146157

Frijda, N. H., Ridderinkhof, K. R., & Rietveld, E. (2014). Impulsive action : Emotional impulses and their control. *Frontiers in Psychology*, *5*. https://www.frontiersin.org/articles/10.3389/fpsyg.2014.00518

Fu, Z., Wu, D.-A. J., Ross, I., Chung, J. M., Mamelak, A. N., Adolphs, R., & Rutishauser, U. (2019). Single-Neuron Correlates of Error Monitoring and Post-Error Adjustments in Human Medial Frontal Cortex. *Neuron*, *101*(1), 165-177.e5. https://doi.org/10.1016/j.neuron.2018.11.016

Gehring, W. J., & Willoughby, A. R. (2002). The Medial Frontal Cortex and the Rapid Processing of Monetary Gains and Losses. *Science*, *295*(5563), 2279-2282. https://doi.org/10.1126/science.1066893

Gipson, C. D., Beckmann, J. S., Adams, Z. W., Marusich, J. A., Nesland, T. O., Yates, J. R., Kelly, T. H., & Bardo, M. T. (2012). A translational behavioral model of mood-based impulsivity : Implications for substance abuse. *Drug and Alcohol Dependence*, *122*(1), 93-99. https://doi.org/10.1016/j.drugalcdep.2011.09.014

Gold, J. I., & Shadlen, M. N. (2007). The Neural Basis of Decision Making. *Annual Review of Neuroscience*, *30*(1), 535-574. https://doi.org/10.1146/annurev.neuro.29.051605.113038

Gottlieb, J., Hayhoe, M., Hikosaka, O., & Rangel, A. (2014). Attention, Reward, and Information Seeking. *The Journal of Neuroscience*, *34*(46), 15497. https://doi.org/10.1523/JNEUROSCI.3270-14.2014

Greenhouse, I. (2022). Inhibition for gain modulation in the motor system. *Experimental Brain Research*, *240*(5), 1295-1302. https://doi.org/10.1007/s00221-022-06351-5

Gross, M. P., & Dobbins, I. G. (2021). Pupil dilation during memory encoding reflects time pressure rather than depth of processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *47*(2), 264-281. https://doi.org/10.1037/xlm0000818

Guo, X., Luo, Z., & Yu, X. (2020). A Speed-Accuracy Tradeoff Hierarchical Model Based on Cognitive Experiment. *Frontiers in Psychology*, *10*. https://www.frontiersin.org/articles/10.3389/fpsyg.2019.02910

Haith, A. M., Reppert, T. R., & Shadmehr, R. (2012). Evidence for Hyperbolic Temporal Discounting of Reward in Control of Movements. *The Journal of Neuroscience*, *32*(34), 11727-11736. https://doi.org/10.1523/JNEUROSCI.0424-12.2012

Hajcak, G., McDonald, N., & Simons, R. F. (2003). To err is autonomic : Error-related brain potentials, ANS activity, and post-error

compensatory behavior. *Psychophysiology*, *40*(6), 895-903. https://doi.org/10.1111/1469-8986.00107

Hajcak, G., & Simons, R. F. (2002). Error-related brain activity in obsessive–compulsive undergraduates. *Psychiatry Research*, *110*(1), 63-72. https://doi.org/10.1016/S0165-1781(02)00034-3

Hanks, T., Kiani, R., & Shadlen, M. N. (2014). A neural mechanism of speed-accuracy tradeoff in macaque area LIP. *eLife*, *3*, e02260. https://doi.org/10.7554/eLife.02260

Hannah, R., & Aron, A. R. (2021). Towards real-world generalizability of a circuit for action-stopping. *Nature Reviews Neuroscience*, *22*(9), 538-552. https://doi.org/10.1038/s41583-021-00485-1

Hawkins, G. E., Forstmann, B. U., Wagenmakers, E.-J., Ratcliff, R., & Brown, S. D. (2015). Revisiting the Evidence for Collapsing Boundaries and Urgency Signals in Perceptual Decision-Making. *The Journal of Neuroscience*, *35*(6), 2476-2484. https://doi.org/10.1523/JNEUROSCI.2410-14.2015

Hawkins, G. E., & Heathcote, A. (2021). Racing against the clock : Evidence-based versus time-based decisions. *Psychological Review*, *128*(2), 222-263. https://doi.org/10.1037/rev0000259

Heitz, R. P. (2014). The speed-accuracy tradeoff : History, physiology, methodology, and behavior. *Frontiers in neuroscience*, *8*, 150.

Henmon, V. A. C. (1911). The relation of the time of a judgment to its accuracy. *Psychological review*, *18*(3), 186.

Herz, D. M., Little, S., Pedrosa, D. J., Tinkhauser, G., Cheeran, B., Foltynie, T., Bogacz, R., & Brown, P. (2018). Mechanisms Underlying Decision-Making as Revealed by Deep-Brain Stimulation in Patients with Parkinson's Disease. *Current Biology*, *28*(8), 1169-1178.e6. https://doi.org/10.1016/j.cub.2018.02.057

Herz, D. M., Tan, H., Brittain, J.-S., Fischer, P., Cheeran, B., Green, A. L., FitzGerald, J., Aziz, T. Z., Ashkan, K., Little, S., Foltynie, T., Limousin, P., Zrinzo, L., Bogacz, R., & Brown, P. (2017). Distinct mechanisms mediate speed-accuracy adjustments in cortico-subthalamic networks. *eLife*, *6*, e21481. https://doi.org/10.7554/eLife.21481

Hilz, M. J. (2022). Transcutaneous vagus nerve stimulation—A brief introduction and overview. *Autonomic Neuroscience: Basic and Clinical*, *243*. https://doi.org/10.1016/j.autneu.2022.103038

Holroyd, C. B., Larsen, J. T., & Cohen, J. D. (2004). Context dependence of the event-related brain potential associated with reward and punishment. *Psychophysiology*, *41*(2), 245-253. https://doi.org/10.1111/j.1469-8986.2004.00152.x

Houtman, F., Castellar, E. N., & Notebaert, W. (2012). Orienting to errors with and without immediate feedback. *Journal of Cognitive*

Psychology, *24*(3), 278-285. https://doi.org/10.1080/20445911.2011.617301

Huang, Y., & Rao, R. P. N. (2013). Reward Optimization in the Primate Brain : A Probabilistic Model of Decision Making under Uncertainty. *PLoS ONE*, *8*(1), e53344. https://doi.org/10.1371/journal.pone.0053344

Jahanshahi, M., Obeso, I., Baunez, C., Alegre, M., & Krack, P. (2015). Parkinson's D isease, the S ubthalamic N ucleus, I nhibition, and I mpulsivity. *Movement Disorders*, *30*(2), 128-140. https://doi.org/10.1002/mds.26049

Kaduk, K., Henry, T., Guitton, J., Meunier, M., Thura, D., & Hadj-Bouziane, F. (2023). Atomoxetine and reward size equally improve task engagement and perceptual decisions but differently affect movement execution. *Neuropharmacology*, *241*, 109736. https://doi.org/10.1016/j.neuropharm.2023.109736

Kahneman, D., & Beatty, J. (1966). Pupil Diameter and Load on Memory. *Science*, *154*(3756), 1583-1585. https://doi.org/10.1126/science.154.3756.1583

Karşılar, H., Simen, P., Papadakis, S., & Balcı, F. (2014). Speed accuracy trade-off under response deadlines. *Frontiers in Neuroscience*, *8*. https://www.frontiersin.org/articles/10.3389/fnins.2014.00248

Kelly, S. P., Corbett, E. A., & O'Connell, R. G. (2021). Neurocomputational mechanisms of prior-informed perceptual decision-making in humans. *Nature Human Behaviour*, *5*(4), 467-481.

Kilpatrick, Z. P., Holmes, W. R., Eissa, T. L., & Josić, K. (2019). Optimal models of decision-making in dynamic environments. *Current Opinion in Neurobiology*, *58*, 54-60. https://doi.org/10.1016/j.conb.2019.06.006

King, J. A., Korb, F. M., von Cramon, D. Y., & Ullsperger, M. (2010). Post-Error Behavioral Adjustments Are Facilitated by Activation and Suppression of Task-Relevant and Task-Irrelevant Information Processing. *The Journal of Neuroscience*, *30*(38), 12759. https://doi.org/10.1523/JNEUROSCI.3274-10.2010

Kirschner, H., Humann, J., Derrfuss, J., Danielmeier, C., & Ullsperger, M. (2021). Neural and behavioral traces of error awareness. *Cognitive, Affective, & Behavioral Neuroscience*, *21*(3), 573-591. https://doi.org/10.3758/s13415-020-00838-w

Kita, K. Du, Y., & Haith, A. M. (2023). Evidence for a common mechanism supporting invigoration of action selection and action execution. Journal of neurophysiology, 130(2), 238–246. https://doi.org/10.1152/jn.00510.2022

Klein, P.-A., Petitjean, C., Olivier, E., & Duque, J. (2014). Top-down suppression of incompatible motor activations during response

selection under conflict. *NeuroImage*, *86*, 138-149. https://doi.org/10.1016/j.neuroimage.2013.08.005

LaBerge, D. (1962). A recruitment theory of simple behavior. *Psychometrika*, *27*(4), 375-396. https://doi.org/10.1007/BF02289645

Laming, D. R. J. (1968). *Information theory of choice-reaction times.* Academic Press.

Lawlor, J., Zagala, A., Jamali, S., & Boubenec, Y. (2023). Pupillary dynamics reflect the impact of temporal expectation on detection strategy. *iScience*, *26*(2), 106000. https://doi.org/10.1016/j.isci.2023.106000

Lemon, W. C. (1991). Fitness consequences of foraging behaviour in the zebra finch. *Nature*, *352*(6331), 153-155. https://doi.org/10.1038/352153a0

Lerche, V., & Voss, A. (2019). Experimental validation of the diffusion model based on a slow response time paradigm. *Psychological Research*, *83*(6), 1194-1209. https://doi.org/10.1007/s00426-017-0945-8

Leroy, É., Koun, É., & Thura, D. (2023). Integrated control of non-motor and motor efforts during perceptual decision-making and action execution : A pilot study. *Scientific Reports*, *13*(1), 9354. https://doi.org/10.1038/s41598-023-36443-3

LeWitt, P. A. (2015). Levodopa therapy for Parkinson's disease : Pharmacokinetics and pharmacodynamics. *Movement Disorders*, *30*(1), 64-72. https://doi.org/10.1002/mds.26082

Li, Q., Long, Q., Hu, N., Tang, Y., & Chen, A. (2020). N-Back Task Training Helps to Improve Post-error Performance. *Frontiers in Psychology*, *11*. https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00370

Liesefeld, H. R., & Janczyk, M. (2019). Combining speed and accuracy to control for speed-accuracy trade-offs(?). *Behavior Research Methods*, *51*(1), 40-60. https://doi.org/10.3758/s13428-018-1076-x

Logan, G. D. (2002). An instance theory of attention and memory. *Psychological Review*, *109*(2), 376-400. https://doi.org/10.1037/0033-295X.109.2.376

Maddox, W. T., & Bohil, C. J. (2004). Probability matching, accuracy maximization, and a test of the optimal classifier's independence assumption in perceptual categorization. *Perception & Psychophysics*, *66*(1), 104-118. https://doi.org/10.3758/BF03194865

Malhotra, G., Leslie, D. S., Ludwig, C. J. H., & Bogacz, R. (2018). Time-varying decision boundaries : Insights from optimality analysis. *Psychonomic Bulletin & Review*, *25*(3), 971-996. https://doi.org/10.3758/s13423-017-1340-6

Mazzoni, P., Hristova, A., & Krakauer, J. W. (2007). Why Don't We Move Faster ? Parkinson's Disease, Movement Vigor, and Implicit Motivation. *The Journal of Neuroscience*, *27*(27), 7105. https://doi.org/10.1523/JNEUROSCI.0264-07.2007

McGinley, M. J., David, S. V., & McCormick, D. A. (2015). Cortical Membrane Potential Signature of Optimal States for Sensory Signal Detection. *Neuron*, *87*(1), 179-192. https://doi.org/10.1016/j.neuron.2015.05.038

Meyniel, F., Sigman, M., & Mainen, Z. F. (2015). Confidence as Bayesian Probability : From Neural Origins to Behavior. *Neuron*, *88*(1), 78-92. https://doi.org/10.1016/j.neuron.2015.09.039

Miletić, S., Boag, R. J., Trutti, A. C., Stevenson, N., Forstmann, B. U., & Heathcote, A. (2021). A new model of decision processing in instrumental learning tasks. *eLife*, *10*, e63055. https://doi.org/10.7554/eLife.63055

Mink, J. W. (1996). THE BASAL GANGLIA : FOCUSED SELECTION AND INHIBITION OF COMPETING MOTOR PROGRAMS. *Progress in Neurobiology*, *50*(4), 381-425. https://doi.org/10.1016/S0301-0082(96)00042-1

Mordkoff, J. T., & Yantis, S. (s. d.). *An Interactive Race Model of Divided Attention*.

Mosher, C. P., Mamelak, A. N., Malekmohammadi, M., Pouratian, N., & Rutishauser, U. (2021). Distinct roles of dorsal and ventral subthalamic neurons in action selection and cancellation. *Neuron*, *109*(5), 869-881.e6. https://doi.org/10.1016/j.neuron.2020.12.025

Mulder, M. J., Keuken, M. C., Van Maanen, L., Boekel, W., Forstmann, B. U., & Wagenmakers, E.-J. (2013). The speed and accuracy of perceptual decisions in a random-tone pitch task. *Attention, Perception, & Psychophysics*, *75*(5), 1048-1058. https://doi.org/10.3758/s13414-013-0447-8

Murphy, P. R., Boonstra, E., & Nieuwenhuis, S. (2016a). Global gain modulation generates time-dependent urgency during perceptual choice in humans. *Nature Communications*, *7*(1), 13526. https://doi.org/10.1038/ncomms13526

Murphy, P. R., Robertson, I. H., Balsters, J. H., & O'connell, R. G. (2011). Pupillometry and P3 index the locus coeruleus–noradrenergic arousal function in humans. *Psychophysiology*, *48*(11), 1532-1543. https://doi.org/10.1111/j.1469-8986.2011.01226.x

Murphy, P. R., van Moort, M. L., & Nieuwenhuis, S. (2016b). The Pupillary Orienting Response Predicts Adaptive Behavioral Adjustment after Errors. *PLOS ONE*, *11*(3), e0151763. https://doi.org/10.1371/journal.pone.0151763

Myers, C. E., Interian, A., & Moustafa, A. A. (2022). A practical introduction to using the drift diffusion model of decision-making in cognitive psychology, neuroscience, and health sciences. *Frontiers in*

Psychology, *13*, 1039172. https://doi.org/10.3389/fpsyg.2022.1039172

Navarro-Cebrian, A., Knight, R. T., & Kayser, A. S. (2013). Error-Monitoring and Post-Error Compensations : Dissociation between Perceptual Failures and Motor Errors with and without Awareness. *The Journal of Neuroscience*, *33*(30), 12375. https://doi.org/10.1523/JNEUROSCI.0447-13.2013

Neubert, F.-X., Mars, R. B., Buch, E. R., Olivier, E., & Rushworth, M. F. S. (2010). Cortical and subcortical interactions during action reprogramming and their related white matter pathways. *Proceedings of the National Academy of Sciences*, *107*(30), 13240-13245. https://doi.org/10.1073/pnas.1000674107

Nigbur, R., & Ullsperger, M. (2020). Funny kittens : Positive mood induced via short video-clips affects error processing but not conflict control. *International Journal of Psychophysiology*, *147*, 147-155. https://doi.org/10.1016/j.ijpsycho.2019.11.007

Niv, Y. (2007). Cost, Benefit, Tonic, Phasic : What Do Response Rates Tell Us about Dopamine and Motivation? *Annals of the New York Academy of Sciences*, *1104*(1), 357-376. https://doi.org/10.1196/annals.1390.018

Notebaert, W., Houtman, F., Opstal, F. V., Gevers, W., Fias, W., & Verguts, T. (2009). Post-error slowing : An orienting account. *Cognition*, *111*(2), 275-279. https://doi.org/10.1016/j.cognition.2009.02.002

Obeso, I., Wilkinson, L., Casabona, E., Bringas, M. L., Álvarez, M., Álvarez, L., Pavón, N., Rodríguez-Oroz, M.-C., Macías, R., Obeso, J. A., & Jahanshahi, M. (2011a). Deficits in inhibitory control and conflict resolution on cognitive and motor tasks in Parkinson's disease. *Experimental Brain Research*, *212*(3), 371-384. https://doi.org/10.1007/s00221-011-2736-6

Obeso, I., Wilkinson, L., & Jahanshahi, M. (2011b). Levodopa medication does not influence motor inhibition or conflict resolution in a conditional stop-signal task in Parkinson's disease. *Experimental Brain Research*, *213*(4), 435-445. https://doi.org/10.1007/s00221-011-2793-x

O'Connell, R. G., Shadlen, M. N., Wong-Lin, K., & Kelly, S. P. (2018). Bridging Neural and Computational Viewpoints on Perceptual Decision-Making. *Trends in Neurosciences*, *41*(11), 838-852. https://doi.org/10.1016/j.tins.2018.06.005

Oldfield, R. C. (1971). The assessment and analysis of handedness : The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97-113. https://doi.org/10.1016/0028-3932(71)90067-4

Park, J., Coddington, L. T., & Dudman, J. T. (2020). Basal Ganglia Circuits for Action Specification. *Annual Review of Neuroscience*, *43*(1), 485-507. https://doi.org/10.1146/annurev-neuro-070918-050452

Pike, R. (1973). Response latency models for signal detection. *Psychological Review*, *80*(1), 53.

Pote, I., Torkamani, M., Kefalopoulou, Z.-M., Zrinzo, L., Limousin-Dowsey, P., Foltynie, T., Speekenbrink, M., & Jahanshahi, M. (2016). Subthalamic nucleus deep brain stimulation induces impulsive action when patients with Parkinson's disease act under speed pressure. *Experimental Brain Research*, *234*(7), 1837-1848. https://doi.org/10.1007/s00221-016-4577-9

Potts, G. F. (2011). Impact of reward and punishment motivation on behavior monitoring as indexed by the error-related negativity. *PROCEEDINGS OF THE 15TH WORLD CONGRESS OF PSYCHOPHYSIOLOGY of the International Organization of Psychophysiology (I.O.P.) Budapest, Hungary September 1-4, 2010*, *81*(3), 324-331. https://doi.org/10.1016/j.ijpsycho.2011.07.020

Pouget, A., Drugowitsch, J., & Kepecs, A. (2016). Confidence and certainty : Distinct probabilistic quantities for different goals. *Nature Neuroscience*, *19*(3), 366-374. https://doi.org/10.1038/nn.4240

Purcell, B. A., & Kiani, R. (2016). Neural Mechanisms of Post-error Adjustments of Decision Policy in Parietal Cortex. *Neuron*, *89*(3), 658-671. https://doi.org/10.1016/j.neuron.2015.12.027

Purves, D. (2001). Modulation of movement by the basal ganglia. *Neuroscience*.

Quoilin, C., Fievez, F., & Duque, J. (2019). Preparatory inhibition : Impact of choice in reaction time tasks. *Neuropsychologia*, *129*, 212-222. https://doi.org/10.1016/j.neuropsychologia.2019.04.016

Rabbitt, P. M. A., & Vyas, S. M. (1970). An elementary preliminary taxonomy for some errors in laboratory choice RT tasks. *Acta Psychologica*, *33*, 56-76. https://doi.org/10.1016/0001-6918(70)90122-8

Rae, B., Heathcote, A., Donkin, C., Averell, L., & Brown, S. (2014). The hare and the tortoise : Emphasizing speed can change the evidence used to make decisions. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*(5), 1226-1243. https://doi.org/10.1037/a0036801

Rafiei, F., & Rahnev, D. (2021). Qualitative speed-accuracy tradeoff effects that cannot be explained by the diffusion model under the selective influence assumption. *Scientific Reports*, *11*(1), 45. https://doi.org/10.1038/s41598-020-79765-2

Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review*, *85*(2), 59-108. https://doi.org/10.1037/0033-295X.85.2.59

Ratcliff, R. (2002). A diffusion model account of response time and accuracy in a brightness discrimination task : Fitting real data and failing to fit fake but plausible data. *Psychonomic Bulletin & Review*, *9*(2), 278-291. https://doi.org/10.3758/BF03196283

Ratcliff, R., & McKoon, G. (1988). A retrieval theory of priming in memory. Psychological review, 95(3), 385–408. https://doi.org/10.1037/0033-295x.95.3.385

Ratcliff, R., & McKoon, G. (2008). The Diffusion Decision Model : Theory and Data for Two-Choice Decision Tasks. *Neural Computation*, *20*(4), 873-922. https://doi.org/10.1162/neco.2008.12-06-420

Ratcliff, R., & Rouder, J. N. (1998). Modeling Response Times for Two-Choice Decisions. *Psychological Science*, *9*(5), 347-356. https://doi.org/10.1111/1467-9280.00067

Ratcliff, R., & Smith, P. L. (2004). A Comparison of Sequential Sampling Models for Two-Choice Reaction Time. *Psychological Review*, *111*(2), 333-367. https://doi.org/10.1037/0033-295X.111.2.333

Ratcliff, R., Smith, P. L., Brown, S. D., & McKoon, G. (2016). Diffusion Decision Model : Current Issues and History. *Trends in Cognitive Sciences*, *20*(4), 260-281. https://doi.org/10.1016/j.tics.2016.01.007

Reddi, B. A. J., Asrress, K. N., & Carpenter, R. H. S. (2003). Accuracy, Information, and Response Time in a Saccadic Decision Task. *Journal of Neurophysiology*, *90*(5), 3538-3546. https://doi.org/10.1152/jn.00689.2002

Reppert, T. R., Heitz, R. P., & Schall, J. D. (2023). Neural mechanisms for executive control of speed-accuracy trade-off. *Cell Reports*, *42*(11), 113422. https://doi.org/10.1016/j.celrep.2023.113422

Reppert, T. R., Lempert, K. M., Glimcher, P. W., & Shadmehr, R. (2015). Modulation of Saccade Vigor during Value-Based Decision Making. *The Journal of Neuroscience*, *35*(46), 15369-15378. https://doi.org/10.1523/JNEUROSCI.2621-15.2015

Reynaud, A. J., Saleri Lunazzi, C., & Thura, D. (2020). Humans sacrifice decision-making for action execution when a demanding control of movement is required. *Journal of Neurophysiology*, *124*(2), 497-509. https://doi.org/10.1152/jn.00220.2020

Rinberg, D., Koulakov, A., & Gelperin, A. (2006). Speed-Accuracy Tradeoff in Olfaction. *Neuron*, *51*(3), 351-358. https://doi.org/10.1016/j.neuron.2006.07.013

Saderi, D., Schwartz, Z. P., Heller, C. R., Pennington, J. R., & David, S. V. (2021). Dissociation of task engagement and arousal effects in auditory cortex and midbrain. *eLife*, *10*, e60153. https://doi.org/10.7554/eLife.60153

ŞAHİN, M., & AYBEK, E. (2020). Jamovi : An Easy to Use Statistical Software for the Social Scientists. *International Journal of*

Assessment Tools in Education, *6*(4), 670-692. https://doi.org/10.21449/ijate.661803

Salamone, J. D., & Correa, M. (2024). The Neurobiology of Activational Aspects of Motivation : Exertion of Effort, Effort-Based Decision Making, and the Role of Dopamine. *Annual Review of Psychology*, *75*(1), annurev-psych-020223-012208. https://doi.org/10.1146/annurev-psych-020223-012208

Saleri Lunazzi, C., Reynaud, A. J., & Thura, D. (2021). Dissociating the Impact of Movement Time and Energy Costs on Decision-Making and Action Initiation in Humans. *Frontiers in Human Neuroscience*, *15*. https://doi.org/10.3389/fnhum.2021.715212

Saleri Lunazzi, C., Thura, D., & Reynaud, A. J. (2023). Impact of decision and action outcomes on subsequent decision and action behaviours in humans. *European Journal of Neuroscience*, *57*(7), 1098-1113. https://doi.org/10.1111/ejn.15932

Salinas, E., Scerra, V. E., Hauser, C. K., Costello, M. G., & Stanford, T. R. (2014). Decoupling speed and accuracy in an urgent decision-making task reveals multiple contributions to their trade-off. *Frontiers in Neuroscience*, *8*. https://www.frontiersin.org/articles/10.3389/fnins.2014.00085

Sanders, J. I., Hangya, B., & Kepecs, A. (2016). Signatures of a Statistical Computation in the Human Sense of Confidence. *Neuron*, *90*(3), 499-506. https://doi.org/10.1016/j.neuron.2016.03.025

Schiffler, B. C., Bengtsson, S. L., & Lundqvist, D. (2017). The Sustained Influence of an Error on Future Decision-Making. *Frontiers in Psychology*, *8*. https://www.frontiersin.org/articles/10.3389/fpsyg.2017.01077

Schroder, H. S., Nickels, S., Cardenas, E., Breiger, M., Perlo, S., & Pizzagalli, D. A. (2020). Optimizing assessments of post-error slowing : A neurobehavioral investigation of a flanker task. *Psychophysiology*, *57*(2), e13473. https://doi.org/10.1111/psyp.13473

Schultz, W., Stauffer, W. R., & Lak, A. (2017). The phasic dopamine signal maturing : From reward via behavioural activation to formal economic utility. *Current Opinion in Neurobiology*, *43*, 139-148. https://doi.org/10.1016/j.conb.2017.03.013

Shadlen, M., Britten, K., Newsome, W., & Movshon, J. (1996). A computational analysis of the relationship between neuronal and behavioral responses to visual motion. *The Journal of Neuroscience*, *16*(4), 1486-1510. https://doi.org/10.1523/JNEUROSCI.16-04-01486.1996

Shadmehr, R., Huang, H. J., & Ahmed, A. A. (2016). A Representation of Effort in Decision-Making and Motor Control. *Current Biology*, *26*(14), 1929-1934. https://doi.org/10.1016/j.cub.2016.05.065

Shadmehr, R., Orban De Xivry, J. J., Xu-Wilson, M., & Shih, T.-Y. (2010). Temporal Discounting of Reward and the Cost of Time in Motor Control. *The Journal of Neuroscience*, *30*(31), 10507-10516. https://doi.org/10.1523/JNEUROSCI.1343-10.2010

Shadmehr, R., Reppert, T. R., Summerside, E. M., Yoon, T., & Ahmed, A. A. (2019). Movement Vigor as a Reflection of Subjective Economic Utility. *Trends in Neurosciences*, *42*(5), 323-336. https://doi.org/10.1016/j.tins.2019.02.003

Shin, H.-W., Kang, S. Y., & Sohn, Y. H. (2007). Disturbed surround inhibition in preclinical parkinsonism. *Clinical neurophysiology*, *118*(10), 2176-2179.

Siegert, S., Herrojo Ruiz, M., Brücke, C., Huebl, J., Schneider, G.-H., Ullsperger, M., & Kühn, A. A. (2014). Error signals in the subthalamic nucleus are related to post-error slowing in patients with Parkinson's disease. *Special issue: What does human intracerebral recording tell us about emotions?*, *60*, 103-120. https://doi.org/10.1016/j.cortex.2013.12.008

Simen, P., Contreras, D., Buck, C., Hu, P., Holmes, P., & Cohen, J. D. (2009). Reward rate optimization in two-alternative decision making : Empirical tests of theoretical predictions. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(6), 1865-1897. https://doi.org/10.1037/a0016926

Simões-Franklin, C., Hester, R., Shpaner, M., Foxe, J. J., & Garavan, H. (2010). Executive function and error detection : The effect of motivation on cingulate and ventral striatum activity. *Human Brain Mapping*, *31*(3), 458-469. https://doi.org/10.1002/hbm.20879

Smith, D. M., Dykstra, T., Hazeltine, E., & Schumacher, E. H. (2020). Task representation affects the boundaries of behavioral slowing following an error. *Attention, Perception, & Psychophysics*, *82*(5), 2315-2326. https://doi.org/10.3758/s13414-020-01985-5

Smith, G. A., & Brewer, N. (1995). Slowness and age : Speed-accuracy mechanisms. *Psychology and aging*, *10*(2), 238.

Smith, P. L., & Vickers, D. (1988). The accumulator model of two-choice discrimination. *Journal of Mathematical Psychology*, *32*(2), 135-168. https://doi.org/10.1016/0022-2496(88)90043-0

Sokolov, E. N. (1963). Higher Nervous Functions : The Orienting Reflex. *Annual Review of Physiology*, *25*(1), 545-580. https://doi.org/10.1146/annurev.ph.25.030163.002553

Soutschek, A., & Tobler, P. N. (2023). A process model account of the role of dopamine in intertemporal choice. *eLife*, *12*, e83734. https://doi.org/10.7554/eLife.83734

Spieser, L., Servant, M., Hasbroucq, T., & Burle, B. (2017). Beyond decision ! Motor contribution to speed–accuracy trade-off in decision-making. *Psychonomic Bulletin & Review*, *24*(3), 950-956. https://doi.org/10.3758/s13423-016-1172-9

Standage, D., You, H., Wang, D., & Dorris, M. (2011). Gain Modulation by an Urgency Signal Controls the Speed–Accuracy Trade-Off in a Network Model of a Cortical Decision Circuit. *Frontiers in Computational Neuroscience*, *5*. https://www.frontiersin.org/articles/10.3389/fncom.2011.00007

Steinemann, N. A., O'Connell, R. G., & Kelly, S. P. (2018). Decisions are expedited through multiple neural adjustments spanning the sensorimotor hierarchy. *Nature Communications*, *9*(1), 3627. https://doi.org/10.1038/s41467-018-06117-0

Steinhauser, M., & Andersen, S. K. (2019). Rapid adaptive adjustments of selective attention following errors revealed by the time course of steady-state visual evoked potentials. *NeuroImage*, *186*, 83-92. https://doi.org/10.1016/j.neuroimage.2018.10.059

Steudel-Numbers, K. L., & Wall-Scheffler, C. M. (2009). Optimal running speed and the evolution of hominin hunting strategies. *Journal of Human Evolution*, *56*(4), 355-360. https://doi.org/10.1016/j.jhevol.2008.11.002

Stone, M. (1960). Models for choice-reaction time. *Psychometrika*, *25*(3), 251-260. https://doi.org/10.1007/BF02289729

Swensson, R. G. (1972). The elusive tradeoff : Speed vs accuracy in visual discrimination tasks. *Perception & Psychophysics*, *12*(1), 16-32.

Swensson, R. G., & Edwards, W. (1971). Response strategies in a two-choice reaction task with a continuous cost for time. *Journal of Experimental Psychology*, *88*(1), 67.

Thura, D. (2020). Decision urgency invigorates movement in humans. *Behavioural Brain Research*, *382*, 112477. https://doi.org/10.1016/j.bbr.2020.112477

Thura, D., Beauregard-Racine, J., Fradet, C.-W., & Cisek, P. (2012). Decision making by urgency gating : Theory and experimental support. *Journal of Neurophysiology*, *108*(11), 2912-2930. https://doi.org/10.1152/jn.01071.2011

Thura, D., Cabana, J.-F., Feghaly, A., & Cisek, P. (2022). Integrated neural dynamics of sensorimotor decisions and actions. *PLOS Biology*, *20*(12), e3001861. https://doi.org/10.1371/journal.pbio.3001861

Thura, D., & Cisek, P. (2014). Deliberation and Commitment in the Premotor and Primary Motor Cortex during Dynamic Decision Making. *Neuron*, *81*(6), 1401-1416. https://doi.org/10.1016/j.neuron.2014.01.031

Thura, D., & Cisek, P. (2017). The Basal Ganglia Do Not Select Reach Targets but Control the Urgency of Commitment. *Neuron*, *95*(5), 1160-1170.e5. https://doi.org/10.1016/j.neuron.2017.07.039

Thura, D., Cos, I., Trung, J., & Cisek, P. (2014). Context-Dependent Urgency Influences Speed–Accuracy Trade-Offs in Decision-Making and Movement Execution. *The Journal of Neuroscience*, *34*(49), 16442-16454. https://doi.org/10.1523/JNEUROSCI.0162-14.2014

Thura, D., Guberman, G., & Cisek, P. (2017). Trial-to-trial adjustments of speed-accuracy trade-offs in premotor and primary motor cortex. *Journal of neurophysiology*, *117*(2), 665-683.

Topor, M., Opitz, B., & Leonard, H. C. (2021). Error-Related Cognitive Control and Behavioral Adaptation Mechanisms in the Context of Motor Functioning and Anxiety. *Frontiers in Human Neuroscience*, *15*. https://www.frontiersin.org/articles/10.3389/fnhum.2021.615616

Trueblood, J. S., Heathcote, A., Evans, N. J., & Holmes, W. R. (2021). Urgency, leakage, and the relative nature of information processing in decision-making. *Psychological Review*, *128*(1), 160-186. https://doi.org/10.1037/rev0000255

Unger, K., Heintz, S., & Kray, J. (2012). Punishment sensitivity modulates the processing of negative feedback but not error-induced learning. *Frontiers in Human Neuroscience*, *6*. https://www.frontiersin.org/articles/10.3389/fnhum.2012.00186

Urai, A. E., Braun, A., & Donner, T. H. (2017). Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nature Communications*, *8*(1), 14637. https://doi.org/10.1038/ncomms14637

Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice : The leaky, competing accumulator model. *Psychological Review*, *108*(3), 550-592. https://doi.org/10.1037/0033-295X.108.3.550

Van den Brink, R. L., Wynn, S. C., & Nieuwenhuis, S. (2014). Post-Error Slowing as a Consequence of Disturbed Low-Frequency Oscillatory Phase Entrainment. *The Journal of Neuroscience*, *34*(33), 11096. https://doi.org/10.1523/JNEUROSCI.4991-13.2014

Van Driel, J., Ridderinkhof, K. R., & Cohen, M. X. (2012). Not All Errors Are Alike : Theta and Alpha EEG Dynamics Relate to Differences in Error-Processing Dynamics. *The Journal of Neuroscience*, *32*(47), 16795. https://doi.org/10.1523/JNEUROSCI.0802-12.2012

Van Zandt, T., Colonius, H., & Proctor, R. W. (2000). A comparison of two response time models applied to perceptual matching. *Psychonomic*

Bulletin & Review, *7*(2), 208-256. https://doi.org/10.3758/BF03212980

Vanunu, Y., & Ratcliff, R. (2023). The effect of speed-stress on driving behavior : A diffusion model analysis. *Psychonomic Bulletin & Review*, *30*(3), 1148-1157. https://doi.org/10.3758/s13423-022-02200-2

Vassiliadis, P., & Derosiere, G. (2020). Selecting and Executing Actions for Rewards. *The Journal of Neuroscience*, *40*(34), 6474. https://doi.org/10.1523/JNEUROSCI.1250-20.2020

Vassiliadis, P., Derosiere, G., Grandjean, J., & Duque, J. (2020). Motor training strengthens corticospinal suppression during movement preparation. *Journal of Neurophysiology*, *124*(6), 1656-1666. https://doi.org/10.1152/jn.00378.2020

Verbruggen, F., Chambers, C. D., Lawrence, N. S., & McLaren, I. P. L. (2017). Winning and losing : Effects on impulsive action. *Journal of Experimental Psychology: Human Perception and Performance*, *43*(1), 147-168. https://doi.org/10.1037/xhp0000284

Voskuilen, C., Ratcliff, R., & Smith, P. L. (2016). Comparing fixed and collapsing boundary versions of the diffusion model. *Journal of Mathematical Psychology*, *73*, 59-79. https://doi.org/10.1016/j.jmp.2016.04.008

Wagenmakers, E.-J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Selker, R., Gronau, Q. F., Dropmann, D., Boutin, B., Meerhoff, F., Knight, P., Raj, A., van Kesteren, E.-J., van Doorn, J., Šmíra, M., Epskamp, S., Etz, A., Matzke, D., … Morey, R. D. (2018a). Bayesian inference for psychology. Part II: Example applications with JASP. *Psychonomic Bulletin & Review*, *25*(1), 58-76. https://doi.org/10.3758/s13423-017-1323-7

Wagenmakers, E.-J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., Love, J., Selker, R., Gronau, Q. F., Šmíra, M., Epskamp, S., Matzke, D., Rouder, J. N., & Morey, R. D. (2018b). Bayesian inference for psychology. Part I: Theoretical advantages and practical ramifications. *Psychonomic Bulletin & Review*, *25*(1), 35-57. https://doi.org/10.3758/s13423-017-1343-3

Wagenmakers, E.-J., Ratcliff, R., Gomez, P., & McKoon, G. (2008). A diffusion model account of criterion shifts in the lexical decision task. *Journal of Memory and Language*, *58*(1), 140-159. https://doi.org/10.1016/j.jml.2007.04.006

Weinstein, A. M. (2023). Reward, motivation and brain imaging in human healthy participants – A narrative review. *Frontiers in Behavioral Neuroscience*, *17*, 1123733. https://doi.org/10.3389/fnbeh.2023.1123733

Wessel, J. R. (2018). An adaptive orienting theory of error processing. *Psychophysiology*, *55*(3), e13041. https://doi.org/10.1111/psyp.13041

Wessel, J. R., & Aron, A. R. (2017). On the Globality of Motor Suppression : Unexpected Events and Their Influence on Behavior and Cognition. *Neuron*, *93*(2), 259-280. https://doi.org/10.1016/j.neuron.2016.12.013

Wessel, J. R., Diesburg, D. A., Chalkley, N. H., & Greenlee, J. D. W. (2022). A causal role for the human subthalamic nucleus in non-selective cortico-motor inhibition. *Current Biology*, *32*(17), 3785-3791.e3. https://doi.org/10.1016/j.cub.2022.06.067

Wickelgren, W. A. (1977). Speed-accuracy tradeoff and information processing dynamics. *Acta Psychologica*, *41*(1), 67-85. https://doi.org/10.1016/0001-6918(77)90012-9

Wilhelm, E., Quoilin, C., Derosiere, G., Paço, S., Jeanjean, A., & Duque, J. (2022). Corticospinal Suppression Underlying Intact Movement Preparation Fades in Parkinson's Disease. *Movement Disorders*, *37*(12), 2396-2406. https://doi.org/10.1002/mds.29214

Williams, P., Heathcote, A., Nesbitt, K., & Eidels, A. (2016). Post-error recklessness and the hot hand. *Judgment and Decision Making*, *11*(2), 174-184. https://doi.org/10.1017/S1930297500007282

Winkel, J., Keuken, M. C., Van Maanen, L., Wagenmakers, E.-J., & Forstmann, B. U. (2014). Early evidence affects later decisions : Why evidence accumulation is required to explain response time data. *Psychonomic Bulletin & Review*, *21*(3), 777-784. https://doi.org/10.3758/s13423-013-0551-8

Xu, B., He, T., Lu, Y., Jia, J., Sahakian, B. J., Robbins, T. W., Jin, L., & Ye, Z. (2022). Locus coeruleus integrity correlates with inhibitory functions of the fronto-subthalamic 'hyperdirect' pathway in Parkinson's disease. *NeuroImage: Clinical*, *36*, 103276. https://doi.org/10.1016/j.nicl.2022.103276

Yeung, N. & Sanfey, A. G. (2004). Independent Coding of Reward Magnitude and Valence in the Human Brain. *The Journal of Neuroscience*, *24*(28), 6258. https://doi.org/10.1523/JNEUROSCI.4537-03.2004

Yeung, N., & Summerfield, C. (2012). Metacognition in human decision-making : Confidence and error monitoring. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1594), 1310-1321. https://doi.org/10.1098/rstb.2011.0416

Yoon, T., Geary, R. B., Ahmed, A. A., & Shadmehr, R. (2018). Control of movement vigor and decision making during foraging. *Proceedings of the National Academy of Sciences*, *115*(44). https://doi.org/10.1073/pnas.1812979115

Yttri, E. A., & Dudman, J. T. (2018). A Proposed Circuit Computation in Basal Ganglia : History-Dependent Gain. *Movement Disorders*, *33*(5), 704-716. https://doi.org/10.1002/mds.27321

Zarrugh, M. Y., Todd, F. N., & Ralston, H. J. (1974). Optimization of energy expenditure during level walking. *European Journal of Applied Physiology and Occupational Physiology*, *33*(4), 293-306. https://doi.org/10.1007/BF00430237

Zemliak, V., & MacInnes, W. J. (2022). The Spatial Leaky Competing Accumulator Model. *Frontiers in Computer Science*, *4*, 866029. https://doi.org/10.3389/fcomp.2022.866029

Zénon, A. (2019). Eye pupil signals information gain. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1911), 20191593. https://doi.org/10.1098/rspb.2019.1593

Zhai, S., Kong, J., & Ren, X. (2004). Speed–accuracy tradeoff in Fitts' law tasks—On the equivalency of actual and nominal pointing precision. *International Journal of Human-Computer Studies*, *61*(6), 823-856. https://doi.org/10.1016/j.ijhcs.2004.09.007

Zhang, S., Lee, M. D., Vandekerckhove, J., Maris, G., & Wagenmakers, E.-J. (2014). Time-varying boundaries for diffusion models of decision making and response time. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.01364