The Price of Deciding:

Balancing Resource Constraints for Optimisation

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À ma famille,

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El doctorado suele referirse como un camino. Un camino que, cuando empieza, parece largo, tan largo que cuesta imaginar su final y preocuparse por él. Así que cuando por fin llegó el final, lo pospuse hasta que el tiempo, que al principio me parecía infinito, se hizo corto y me apremió a concluirlo. No diría que lo difícil fue el camino, sino el hecho de llegar a una conclusión, de cerrar todas esas preguntas abiertas y plasmarlas en un papel (o en el teclado de un ordenador). En efecto, si la investigación se reduce a veces a encontrar y comprender, a menudo parece añadir dudas a las certezas. Sin embargo, aunque la duda es generalmente algo negativo, también permite una creatividad y un rigor indispensables en un doctorado, y se convierte en algo increíblemente estimulante cuando se está bien acompañado. He tenido mucha suerte en este sentido, y por fin, llegado al final del camino, me gustaría agradecer a todos los que han sido de cerca o lejos mis compañeros de ruta.

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y con mucho orgullo sobre todas las maravillosas personas que he podido encontrar.

Et pourtant, tout demeure, il suffit de se poser la question : "Que sommes-nous venus faire sur cette Terre" ? La réponse me paraît facile : apprendre, apprendre pour aller vers la connaissance d'un mystère et non pas seulement se contenter de savoir, de se servir avant de servir.

JACQUES PUISAIS

Abstract

Making decisions is an unavoidable yet challenging aspect of life. Amidst a sea of options, one must weigh valuable alternatives, dealing with the frustration of forgoing the majority of them and confront the anxiety of potential wrong choices. This challenge is further compounded by the limitations of finite internal (memory, attention, energy) and external resources (time, money) available for gathering information before reaching a decision. How, then, do individuals adeptly navigate these complexities?

This research probes three distinctive cases demanding a subtle balance between efficient default behaviours and more resourcedemanding but flexible strategies. It reveals humans' capacity to employ strategies aptly engaging costly cognitive control mechanisms or relying instead on prior knowledge (Chapter I). Additionally, these strategies adeptly consider available resources and environmental contexts, while embracing frugal heuristics (Chapter II). Furthermore, our results delineate structured search strategies driven by specific goals, transcending a mere focus on reward maximisation (Chapter III).

Through novel experimental designs mirroring real-life scenarios with naturalistic stimuli, multiple alternatives, and active information search, this research unveils intricate decision-making strategies characterised by adaptability, anticipation, and judicious integration of contextual and intrinsic information. This work lays a foundational framework for understanding the multifaceted factors that modulate human choice behaviour in complex environments.

Keywords: decision-making, EEG, cognitive-control, breadthdepth dilemma, information search, fluctuations

Resum

Prendre decisions es un repte, i a la par un aspecte inevitable a les nostres vides. D'entre totes les opcions viables, hom ha de sotmetre a escrutini i avaluació les diverses alternatives en tant gestionant la frustració adherida a la renuncia de la multitud rebutjada i l'angoixa de la potencial elecció mal presa. Aquest repte es veu accentuat per la disponibilitat finita dels recursos interns (memòria, atenció, energia) i externs (temps, diners), els quals son un agent limitant alhora de recopilar informació necessària per arribar a una decisió. Aleshores, com ho fan les persones per a navegar de forma adaptativa aquesta tasca tan complexa?

Aquesta recerca explora tres situacions que exigeixen un equilibri subtil entre l'actuació de comportaments automàtics i estratègies més costoses en recursos però alhora més flexibles. Els resultats revelen que l'ésser humà es capaç d'utilitzar estratègies que involucren mecanismes de control cognitius costosos o, en comptes, basant-se en coneixements prèviament adquirits (Capítol I). A més, aquestes estratègies tenen en compte els recursos disponibles i el context, mentre adopten heurístiques econòmiques (Capítol II). Addicionalment, els nostres resultats descriuen estratègies estructurals guiades per objectius específics, en comptes de focalitzar-se en la maximització de la recompensa del joc (Capítol III). Gràcies a l'enginyós i novedós dissenv experimental, el qual fa mímica d'escenaris ecològics incorporant estímuls naturalístics, alternatives múltiples i d'una recerca d'informació activa, aquest treball mostra estratègies de presa de decisions complexes, caracteritzades per l'adaptabilitat, l'anticipació i la capacitat d'integrar de manera aclaridora la informació interna i contextual. Aquesta tesi construeix les bases d'un marc conceptual per a l'estudi de la varietat de factors que modulen la presa de decisions dels humans en àmbits complexos.

Paraules clau: presa de decisions, EEG, control cognitiu, dilema amplitud-profunditat, cerca d'informació, fluctuacions

Résumé

Prendre des décisions est un aspect essentiel, bien que difficile, du quotidien. Devant un large éventail d'options, il est crucial de distinguer les plus prometteuses tout en confrontant la frustration de renoncer à la plupart d'entre elles et l'anxiété liée à la perspective d'un choix erroné. Ce défi est accentué par l'accès limité aux ressources internes (mémoire, attention, énergie) et externes (argent, temps) nécessaires pour recueillir des informations et prendre une décision éclairée. Comment, alors, les individus surmontent-ils habilement ces enjeux ?

Cette recherche explore trois situations qui exigent un équilibre subtil entre l'utilisation de comportements automatiques efficaces et des stratégies plus couteuses en ressources mais flexibles. Les résultats révèlent que l'Homme est capable d'utiliser des stratégies engageant de manière judicieuse des mécanismes de contrôle cognitif coûteux ou s'appuyant plutôt sur des connaissances préalablement acquises (Chapitre I). De plus, ces stratégies considèrent habilement les ressources disponibles et le contexte, tout en adoptant des heuristiques économes (Chapitre II). En outre, nos résultats décrivent des stratégies structurées guidées par des objectifs spécifiques, qui dépassent le simple but de maximiser les récompenses en jeu (Chapitre III).

Grâce à l'utilisation de designs expérimentaux novateurs reflétant des scénarios réalistes, incorporant des stimuli naturalistes, de multiples alternatives et une recherche active d'information, ces travaux dévoilent des stratégies complexes de prise de décision caractérisées par leur adaptabilité, leur anticipation et l'intégration opportune d'informations contextuelles et intrinsèques. Ce travail pose les bases d'un cadre conceptuel pour mieux appréhender la variété de facteurs qui interagissent au sein d'environnements complexes et modulent nos choix.

Mots clés: prise de décision, EEG, contrôle cognitif, dilemme largeur-profondeur, recherche d'informations, fluctuations

Choisir, c'était renoncer pour toujours, pour jamais, à tout le reste et la quantité nombreuse de ce reste demeurait préférable à n'importe quelle unité.

ANDRÉ GIDE - Les Nourritures terrestres (1897)

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1. GENERAL INTRODUCTION

Life unfolds as a myriad of choices, ranging from the mundane to the profound. What to wear, what to eat, where to live, what to vote or believe in - each decision, regardless of its apparent significance, shapes our lives in foreseeable and unforeseeable ways; the consequences of our choices are sometimes immediately tangible, but often extend into the realms of uncertainty, introducing complexities that challenge our decision-making abilities.

Even seemingly trivial decisions, such as choosing an outfit for the day, can have far-reaching implications. A wrong choice might render us vulnerable to catch a cold or create discomfort in social interactions. The unpredictability of outcomes further compounds the challenge; unexpected rain can turn a well-planned day into a soggy ordeal. In sum, decisions carry inherent risks and potential opportunities, uncertainties and fears of erring. Balancing these elements, especially as the temporal horizon extends into the future, makes the act of choosing a formidable cognitive task.

Moreover, the fear of making a wrong choice is accompanied by the fear of missed opportunities. Every decision involves selecting one path and forsaking countless others, a process laden with emotional weight. Technological and ethical progress, while expanding our possibilities and improving our well-being (Schwartz, 2016), paradoxically also adds to the burden. While the plethora of alternatives available today drive infinite desire, our capacity to satisfy it remains limited. This notion, is well described in a mechanism called *choice overload* and implies that an abundance of choices can overwhelm, diminishing satisfaction and hampering effective decision-making (Iyengar & Lepper, 2000; Schwartz, 2016). A similar effect is found when decision makers face an amount of information that is greater to what they can process – *information overload* –, negatively affecting the speed and quality of choices (Eppler & Mengis, 2004).

Given the complexity of the decision-making process itself, and the ever-increasing range of choices we are confronted with: how do humans cope with the costs of deciding? This dissertation delves into the intricate processes of human decision-making, exploring the strategies employed to navigate the limited resources required for deciding and their implications on performance. Choosing cannot simply be avoided, and tergiversating should be minimized to gain efficiency. Therefore, understanding how humans grapple with decision-making costs becomes paramount.

1.1. Decisions are costly: exploring the internal and external resource limitations

Before deciding, we need to make an investment in order to gather information about the possible alternatives (Hauser & Wernerfel,

1990). This investment comes at a cost. In terms of internal resources, it draws on cognitive abilities reflected in limited working memory capacity and attention span (Shaw & Shaw, 1977; Bradbury, 2016). Indeed, when bombarded with a multitude of visual stimuli or auditory events or objects, our cognitive architecture allows us to retain only a subset of them, typically around four items (Cowan, 1998; Vogel et al., 2001). Furthermore, the allocation of attentional resources to these items dictates the precision with which they are perceived and remembered, exemplifying the delicate balance we must strike in utilizing our cognitive resources (Bays & Husain, 2008). In their famous example, Simons and Chabris (1999) showed that a stimulus as conspicuous as a walking gorilla may pass entirely unnoticed if one's attention is strongly engaged on a distracting task. Additionally, tasks demanding intensive internal resources often correlate with diminished performance (Norman & Bobrow, 1975). Factors such as task switching (Monsell, 2003), multitasking (Meyer & Kieras, 1997), task complexity (Liu & Li, 2012) or task difficulty (Maynard & Hakel, 1997) including memory load (Rypma et al., 2002) are known to tax our cognitive resources. Mental fatigue, a consequence of prolonged cognitive engagement also adversely affects both cognitive (Boksem et al., 2005; Lorist et al., 2005) and physical performance (Marcora et al., 2009) underscoring the limitation of our internal cognitive reservoirs. Finally, deciding has been shown to be particularly depleting in terms of cognitive

resources, exceeding deliberating or decisions formation (Vohs et al., 2008).

In everyday life, the decisions we make are further confined by external constraints. Time, often a precious and scarce commodity, compels rapid decision-making. Financial limitations add an additional layer of complexity, shaping the choices available to us. Accessibility to essential resources, such as raw materials for energy production and water, poses constraints that reverberate across populations, including the jeopardy of global food security (Hanjra & Qureshi, 2010). Moreover, decisions are profoundly influenced by information, yet this information does not circulate naively. The advent of social media and artificial intelligence (AI), steered by enigmatic algorithms, exposes us to targeted data. This tailored information not only moulds our thoughts but also exerts significant influence, affecting consumer choice (Stephen, 2016) and even swaying political outcomes (Allcott & Gentzkow, 2017; Gorodnichenko et al., 2021). As Y.N. Harari (2017) suggests, « In ancient times having power meant having access to data. Today having power means knowing what to ignore » (p. 462). In this context, the way we allocated our limited resources to search for and consider or overlook new information is essential to overcome meddling, fostering critical thinking and informed decision-making.

These constraints, operative at both individual and societal levels, pose substantial challenges. Understanding how efficiently humans navigate these limitations is imperative, given the profound implications at stake.

1.2. Dealing with the costs of deciding

In the real world, decision-making seldom unfolds in isolation; we are often compelled to respond to multiple stimuli simultaneously. For instance, answering a colleague's question while walking to the cafeteria. If we are familiar with the path, choosing between turning left or right while maintaining the conversation poses no challenge. However, uncertainty about the route may necessitate a momentary pause in the conversation for careful consideration. Similarly, environmental factors beyond our control, such as the delightful distraction of a passing puppy during a conversation, can disrupt our focus, slowing our input in the dialogue. These instances of interference, whether arising from multitasking (Shaffer, 1975) or competing stimuli (Eriksen & Eriksen, 1974) or stimuli features (Stroop, 1935; Simon, 1969), have been extensively studied. They have not only shed light on the complexities of human cognition but have also delineated the distinctions between automatic and controlled processes (Posner & Snyder, 1975; Shiffrin & Schneider, 1977).

Early theories classified automatic processes as rapid, stimulusdriven responses that can be executed in parallel and at no or little cognitive cost. In contrast, controlled processes were deemed voluntary, goal-oriented, slower, and subject to a central limitation in information-processing capacity, compelling them to operate serially.

Striking the right balance between automatic and controlled processes is crucial for efficient interaction with the world, ensuring seamless decision-making even in complex and distracting environments.

a. Automatic processes: efficient but not always relevant

To navigate the intricate web of stimuli and choices that surround us, we often rely on automation, a key strategy that enables efficient responses without demanding active attention. It offers the advantage of speed and the ability to manage multiple tasks concurrently, allowing us to walk while engaged in a conversation or effortlessly perform routine actions. It is essential to perceive automatic and controlled processes not as discrete entities but as part of a spectrum. Through practice, behaviours become automatic and tend to rely less on cognitive control (Garner & Dux, 2015; Ruthruff et al., 2006; Strobach & Torsten, 2017). For instance, a novice driver might struggle to chat while driving, but with practice, these tasks can be seamlessly executed simultaneously. Usual necessary tasks can be performed more efficiently through learning which gives rise to dedicated representations that function independently, enabling parallel processing without interference.

Additionally, automaticity permeates information gathering, as some specific attributes and types of stimuli trigger these automatic processes, a phenomenon called attentional capture. Attentional capture is stronger for salient stimuli such as loud sounds (Corbetta & Shulman, 2002; Theeuwes, 2010), arousing pictures (Schimmack, 2005), emotional cues, especially those indicating potential threats like fearful facial expressions (Anderson et al., 2003), sounds linked to imminent danger (Koster et al., 2004), or moving insects (Carretié et al., 2009). Relevant stimuli are also processed in priority, such as your own name (Berlad & Pratt, 1995) and this even when sleeping (Portas et al., 2000). This swift attentional capture essential for survival and adaptive behaviour, allowing us to respond rapidly to life-threatening situations or react efficiently to important environmental features.

Yet, there's a caveat. Sometimes, these salient stimuli command our attention even if irrelevant to our immediate goals. This phenomenon occurs with stimuli associated with higher subjective value (Anderson et al., 2011; Anderson, 2013), impacting subsequent information processing (Anderson, 2016) and decision-making (Armel et al., 2008; Krajbich et al., 2010; Orquin & Mueller

Loose, 2013). Automatic attentional capture, while efficient, can distract from the task at hand and introduce biases into decisionmaking processes. Studies have shown that, for instance, human choices tend to be faster and more frequently directed towards the alternative associated with the higher reward, even when representing the incorrect response (Afacan-Seref et al., 2018; Corbett et al., 2023; Summerfield & Koechlin, 2010; Noorbaloochi et al., 2015).

This interplay highlights the need for a balance between swift but rigid automatic processes and flexible but slow controlled processes. Cognitive control is crucial in this equation; it steps in to flexibly adjust decisions to the current goal, ensuring that efficiency does not come at the expense of accuracy and adaptability. This balance is the linchpin of effective decision-making in the face of complex and dynamic environments.

b. Cognitive control: flexible but limited

Controlled processes, despite being slower (Kahneman, 2011) and effortful compared to automatic ones, have the advantage to be extremely flexible. They stand as a remarkable feature of human cognition, endowing us with the ability to selectively focus attention and cognitive resources, parsing the environment efficiently with a specific task in mind. Among its many roles, cognitive control allows to hold appealing responses (Donders, 1969), ignoring the

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many distractions (Lavie, 2010), or resisting the multiple temptations surrounding us. It stops us from realising an impulsive purchase (Baumeister, 2002) or grabbing an enticing marshmallow (Mischel et al., 1989), therefore overcoming immediate desires in the pursuit of more distant but greater goals. This mechanism is marked by a broad flexibility, facilitating swift adaptation to novel situations and the development of sophisticated adaptive behaviours, some of which might never have been encountered before (Meiran et al., 2015).

Yet, this extraordinary ability has boundaries. Humans struggle to perform two tasks demanding cognitive control simultaneously, even when these tasks could be executed smoothly in isolation, such as writing dictated words while reading aloud (Shaffer, 1975). The reasons for this limitation are still under debate (Musslick & Cohen, 2021), with recent approaches challenging the conventional view of a central limited capacity, assuming instead, as proposed in early theories of attention (Navon & Gopher, 1979; Allport, 1980), that multiple independent local resources coexist. One such theory posits that multiple tasks share common neural representations, which support generalisation of learned knowledge to future novel situations but may also lead to potential cross-talks between tasks conducted simultaneously (Feng et al., 2014; Musslick et al., 2016). This perspective suggests that limitations in cognitive control are necessary to minimise potential interferences. Additionally, this could also explain attentional or working memory capacity limitations as a way to enforce a small number of alternatives than can be simultaneously considered which may facilitate comparisons and decisions (Cowan, 2010).

The neural basis of cognitive control has been repeatedly attributed to the frontal cortex and especially the dorsal anterior cingulate cortex (dACC) and the lateral prefrontal cortex (lPFC) (M. Botvinick et al., 2004; Ridderinkhof et al., 2004) to play a role in detecting the need for control and implementing behavioural adjustments. Nevertheless, understanding the mechanisms dictating when cognitive control should be applied remains a challenge. Initial theories proposed that the evaluation of the demand for control may be through conflict monitoring, as measured by increased dACC activation in response to conflict in information processing (Botvinick et al., 1999, 2004; Botvinick, 2007). A more recent theory expands this notion, asserting that engaging cognitive control is not solely dictated by the need for control but also integrates the costs and benefits at stake (Shenhav et al., 2013, 2017). This motivational perspective considers the effort associated with cognitive control, balancing its level and type of engagement against the expected value. In essence, cognitive control is not deployed haphazardly; it is strategically allocated, calibrated to the effort demanded and the potential benefits reaped, offering a

nuanced understanding of the interplay between our cognitive abilities and the complexities of the tasks at hand.

1.3. Balancing flexibility and efficiency

a. Value-biased decisions: when does control take the reins?

Humans are often referred to as "cognitive misers" (G. Allport, 1954) as they instinctively avoid unnecessary mental exertion (Taylor, 1981; Kool et al., 2010). Simultaneously, they are driven by a desire to maximise outcomes (von Neumann & Morgenstern, 1944), showcasing a delicate dance between conserving cognitive effort and maximising rewards. Indeed, research demonstrates human ability to adjust cognitive and physical efforts based on anticipated outcomes, enhancing decision accuracy (Bonner & Sprinkle, 2002; Krawczyk et al., 2007; Engelmann et al., 2009; Kouneiher et al., 2009; Kool et al., 2010; Padmala & Pessoa, 2011; Schmidt et al., 2012; Westbrook & Braver, 2015). This intricate interplay extends to working memory and cognitive control, where their precision and engagement respectively are bolstered by expected rewards and the behavioural relevance of the remembered items and task performance (Klyszejko et al., 2014; Frömer et al., 2021). Thus, the level of cognitive control engagement seems to vary with the expected value of control, balancing reward magnitude and control efficacy against the cost of cognitive effort. This theory revisits the negative relationship between mental fatigue

and performance. It suggests that decreased motivation to engage cognitive resources may occur when the costs are perceived to outweigh the predicted rewards (Boksem & Tops, 2008). Additionally, the expected value of control model clarifies how previously acquired knowledge may influence the amount of control exerted (Bustamante et al., 2021; Lieder et al., 2018).

Conflict monitoring and value-biases during decision-making tasks have mostly been studied using simple artificial stimuli such as moving dots (Corbett et al., 2023), grating patterns (Summerfield & Koechlin, 2010; Feuerriegel et al., 2021), or colour shades (Afacan-Seref et al., 2018; Blangero & Kelly, 2017; Carter & van Veen, 2007). In the first chapter of this thesis, I present a study in which we developed a more ecological paradigm to investigate the role played by cognitive control in overcoming automatic processing of subjective value. This approach, using complex choices involving naturalistic stimuli, also enables to shed light on the diverse factors influencing the engagement of control, thus getting closer to the rich interactions that characterise real lifescenarios.

Furthermore, within an additional appendix chapter, our objective was to pinpoint the precise brain regions signalling an elevated demand for cognitive control. This was pursued by analysing intracortical electroencephalography (iEEG) data obtained from an epileptic patient undertaking the same task.

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b. Trade-off in the resource allocation: does it reflect optimal performance?

This optimisation mechanism governing the exertion of control based on expected costs and benefits collides with the idea that limits of human cognitive abilities are measured through their capacity to implement optimal behaviour, meaning following a strategy that maximise the expected reward. According to this view, humans have shown to be sup-optimal in numerous cases, following heuristics (Gigerenzer & Goldstein, 1996; Thorngate, 1980; Shah & Oppenheimer, 2008; Gigerenzer & Gaissmaier, 2011) or basing their strategy on previously acquired knowledge (stereotypes: Allport, 1954) without fully integrating the context they are in. Though, ignoring part of the information present (Macrae et al., 1994) and using simplified strategies (Shugan, 1980) may be a way to reduce the decision making cost.

These behaviours may therefore reflect a wise balance between more automatic or learned strategies and controlled behaviours more flexible but also more costly, instead of a purely limited cognitive capacity. This optimisation under constrains of limited resources is defined as *bounded rationality* (H. A. Simon, 1955; Griffiths et al., 2015) where making optimal use of finite external and internal capacity reflects the rational use of these resources (Lieder & Griffiths, 2020) and may underly observed biases in decision making (Lieder et al., 2018).

This is reflected in numbers of trade-offs, people for example adapt to the time pressure by considering less information or less alternatives at the cost of accuracy (Payne et al., 1993; Gold & Shadlen, 2002). The number and precision of representations that can be actively maintained in working memory may also be modulated (Ma et al., 2014), such as the number of alternatives that one considers, leading to most of them being ignored in consumer choice (Herbig & Kramer, 1994). Instead, other evidence shows that when allocating finite capacity, be it time or financial resources, humans tend to follow a 1/N rule where they equally split their resources among the N alternatives (Benartzi & Thaler, 2001; Hertwig et al., 2002), a trade-off known as the equality heuristics (Messick, 1993).

In the second chapter of this thesis, I present a study addressing the balance between heuristics and resource-intensive but flexible strategies in allocating finite search capacity. Do individuals consider the number of alternatives that maximises expected rewards? Do they adopt heuristics simplifying computations but potentially compromising performance? We address these questions by developing a novel experimental paradigm – the Apricot Breadth-Depth dilemma - where search resources are experimentally parametrised, as opposed to attention or memory, and optimal strategies easily traceable.

c. Fluctuations in resource allocation: controlled or stochastic variability?

The balance between flexibility and efficiency may also be underlying the inherent variability observed in behaviour (Rahnev & Denison, 2018; Renart & Machens, 2014). Fluctuations in the resource allocation may occur due to attentional or motivational variability over time but they may also be intended. Indeed, human intelligence is frequently associated with its ability to respond adaptively in unfamiliar and intricate surroundings in which planning play an important role (Kryven et al., 2021). Anticipating is indeed necessary to make the best of finite resources (monthly budget, food bought for the week, daily energy, etc) (Callaway et al., 2021). Consider for example planning a road trip, it demands meticulous allocation of time across multiple stops, all while ensuring punctual arrival at destinations. In this scenario, one might opt to adhere to the equality heuristic, dedicating equal time to each location. Alternatively, time could be allocated disparately among different stops, possibly even bypassing one stage to allow for a more extended stay at another.

This foresight, while often pivotal for ensuring seamless holidays, comes at a price, necessitating substantial demands on memory,

computational power, and time. Individual traits may shape the extent to which individuals engage in planning and the strategies they adopt (Beach & Mitchell, 1978; Miyake & Friedman, 2012). Indeed, beyond the pursuit of optimizing anticipated outcomes, fluctuations in resource allocation may signify a real-time need to acquire more information, mitigating risks, or experimenting with new strategies to satiate curiosity.

In the third chapter of this thesis, I present a study addressing whether endogenous fluctuations in the allocation of limited resources impact performance. Do they reflect stochastic or intended behaviours? Do they represent strategies designed to optimise objectives beyond the narrow confines of pure reward maximisation? We investigate these questions using an extension of the Apricot Breadth-Death dilemma where humans have to manage limited search capacity other multiple consecutive decisions.

In everyday life, decisions are inescapable; every action, every thought, shapes a trajectory, whether intentional or unintentional, which will influence the future. However, finite cognitive resources and external factors such as time impose limits, restricting our possibilities. Not all paths can be pursued, making choice both challenging and significant. Until not long ago, decision making was studied under simplified protocols involving, typically, two alternatives forced choices between options with a few controlled features and an immediate temporal horizon. More recent work has tried to approximate other real-world decision-making scenarios by expanding the number of choices, their complexity and the temporal horizon (Maselli et al., 2023). This thesis aims to gain a better comprehension of how humans contend with the cost of decisionmaking and manage the allocation of these limited resources, and how this process impacts performance. First, we examine the targeted engagement of cognitive control in counteracting automatic behaviour, underlying a precious adaptability. Secondly, we explore the trade-offs followed by individuals to gain information when faced with numerous alternatives, too many to be thoroughly considered. Finally, we investigate the presence of fluctuations in resource allocation over time and their relationship with performance and intentionality.

2. Chapter I: THE ROLE OF CONFLICT MONITORING IN OVERCOMING VALUE BIASES IN HUMAN DECISION-MAKING

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The role of conflict monitoring in overcoming value biases in human decision-making

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Abstract

The value associated with response alternatives has been observed to impact rapid choices while slower decisions remain relatively unbiased. Here we aim to understand how the decision process is redirected towards goal-relevant evidence after the initial value prioritisation and propose that conflict detection and cognitive control serve as the underlying mechanism. We recorded electroencephalography (EEG) from participants performing a speeded binary choice task based on the price of realistic food stimuli that naturally also encompassed subjective preferences. Our findings indicate that preferred alternatives were consistency selected faster, irrespective of the amount of task-relevant information available and in the absence of any motor or attentional anticipation, suggesting fast automatic integration of value-based information. Furthermore, participants' pre-existing mental representations of item prices and preferences influenced the degree of value biases on response accuracy. Consistent with our initial hypothesis, results show that in incongruent trials, where subjective value and objective information compete, mid-frontal theta (MFT) activity was heightened and predicted choice accuracy, indicating monitoring and detection of conflict. Additionally, our findings unveiled enhanced MFT power proportional to the potential cost opportunity of the choice and following errors, highlighting the implication of cognitive control in various aspects of decisionmaking. In essence, this study provides the foundation for comprehending how value-biases are overcame within the brain, while illustrating the need to use more ecological paradigms to better understand the multifaceted interactions characterising human behaviour in real-world scenarios

Key words: decision-making, value bias, conflict monitoring, EEG, cognitive control, prior

Highlights

- Value biases observed in choice behaviour suggest the fast automatic integration of value-based evidence, even when irrelevant for the current goal and in the absence of any attentional or motor anticipation.
- Preferred alternatives are consistently selected faster than non-preferred alternatives.
- Participants' pre-existing representations of the item prices and preferences influenced the degree of value biases on response accuracy.
- In incongruent trials, mid-frontal theta activity (4-7Hz) is heightened and predicts choice accuracy, indicating monitoring and detection of conflict.
- Increased mid-frontal theta power is also observed proportional to the potential cost opportunity of the choice and following errors, highlighting the implication of cognitive control.
- The classical drift-diffusion model fails to reproduce the value biases observed on choice behaviour.

Introduction

It is midnight, and tomorrow morning you are about to embark on your well-deserved holiday trip to relax. However, you find yourself stressing about what to pack and what not to, and struggling to close the suitcase lid. How did you get yourself into this problem? While it is obviously essential to close your suitcase before your flight, it feels no less important to pack essential clothing, novels you have postponed for months, and of course, your brand-new snorkelling gear. The subjective value you associate with these items and the objective considerations regarding their volume and weight must be all considered together under one single optimization problem. This is the kind of decision-making problem we address here.

In real-life decision making, interactions between values (often subjectively assigned such as preferences) and objective attributes, be them purely physical such as size and weight or more abstract such as monetary costs, are pervasive. In controlled laboratory protocols, previous research has highlighted that items associated with higher value have higher salience in attention tasks (Anderson et al., 2011; Hickey et al., 2011; Libera & Chelazzi, 2006; Theeuwes & Belopolsky, 2012). Beyond attentional capture, the relative values of alternatives also have been shown to impact decision processes (Afacan-Seref et al., 2018; Summerfield & Koechlin, 2010; Blangero & Kelly, 2017; Corbett et al., 2023), with choice alternatives associated with higher value being chosen more often and faster, seemingly regardless of the choice's difficulty (Noorbaloochi et al., 2015).

These findings come as no surprise, considering that we perceive and interact with the world around us through the lens of our internal preferences and desires, which have a strong influence on expected and actual rewards (or punishment) outcomes associated with our actions. The ongoing internal consideration of value, even in the absence of conscious awareness, is further supported by research demonstrating the widespread and automatic nature of the value-based system (VBS), which encompasses a network of brain regions including the ventromedial prefrontal cortex, hippocampus, ventral striatum, and posterior cingulate cortex. Activation of this system occurs during the process of valuation and decision-making based on subjective preferences. The generality of the VBS is supported by its responsiveness to a wide variety of stimuli, such as food items (Plassmann et al., 2007), paintings (Kawabata & Zeki, 2004), sculptures (Dio et al., 2007), faces (O'Doherty et al., 2003), indoor and outdoor scenes (Yue et al., 2007), and houses (Lebreton et al., 2009). Moreover, the activation of the VBS areas during decisions where value is irrelevant to the task at hand strongly suggests that it is engaged automatically (Kim et al., 2007; Lebreton et al., 2009).

Past research has identified brain regions that are sensitive to both choice-relevant and choice-irrelevant value information, and may even predict the extent to which value biases the decision-making process (Grueschow et al., 2015; Hickey et al., 2010). In contrast, other brain areas, such as the medial prefrontal cortex (mPFC), exhibit stronger encoding of value when it is directly relevant to the ongoing decision (Grueschow et al., 2015; Frömer et al., 2019). While certain regions encode value consistently, some prefrontal areas are capable of integrating contextual information about the decision, although this integration process requires time. Previous studies investigating value biases in decisions have demonstrated that as response times slow down, the impact of subjective value on decision-making declines (Afacan-Seref et al., 2018; Noorbaloochi et al., 2015; Summerfield & Koechlin, 2010). These findings suggest the presence of a mechanism that regulates the decisionmaking process, redirecting resources towards pondering goalrelevant evidence after an initial jolt toward value.

Cognitive control emerges as a promising candidate to fulfil this regulatory function. This adaptive mechanism enables individuals to adjust to changing task demands and optimize performance. It relies on the activation of an extensive brain network, which includes prefrontal structures such as the dorsal anterior cingulate cortex (dACC), dorsolateral prefrontal cortex (dIPFC), and the mPFC (M. Botvinick et al., 1999; Debener et al., 2005; Kerns et al., 2004;

MacDonald et al., 2000: Pochon et al., 2008: Sheth et al., 2012). These brain regions increase their activation during conflicting choices or following errors, and it has been postulated that they act as an alert system to facilitate attention reallocation or increase the motor threshold (M. Botvinick et al., 2001; Cavanagh et al., 2012; Guan et al., 2023). In addition to its involvement in cognitive control, the dACC has also been associated with other mechanisms such as information sampling (Monosov & Rushworth, 2022; Boroujeni et al., 2021) and foraging behaviours (Hayden et al., 2011; Kolling et al., 2012; Monosov et al., 2020), and it has been suggested to play a role in perception via 'internal foraging' (Safavi & Dayan, 2022). Moreover, the dACC has been linked to rewardbased decision-making (Bush et al., 2002; Kennerley et al., 2006) and motivation (M. Botvinick & Braver, 2015; Holroyd & Yeung, 2012), and recent research has made strides in reconciling these findings with its role in cognitive control, aiming to develop a global understanding of the dACC's functions.

An emerging perspective posits that the dACC dynamically modulates its activity based on the expected value of control, which is influenced by both task demands and contextual factors such as reward contingencies and task difficulty (Shenhav et al., 2013, 2016). By flexibly adjusting the level of engagement of other brain areas, the dACC optimises the allocation of cognitive resources, maximising the potential benefits of control while minimizing associated costs. This framework primarily relies on functional neuroimaging data, but recent efforts have sought to integrate findings from single-cell recordings and lesion studies conducted in both humans and non-human animals (Silvetti et al., 2011; Holroyd & McClure, 2015; Brown & Alexander, 2017).

Human EEG studies have put forth mid-frontal theta oscillations (MFT, 4-7Hz) as a potential indicator signalling the need for cognitive control (Cavanagh & Frank, 2014). Increased MFT activity has been consistently observed in various scenarios that necessitate heightened cognitive control, including higher cognitive load during working memory tasks (Itthipuripat et al., 2013; Onton

et al., 2005), sustained attention (Sauseng et al., 2007), conflicting stimuli (Nigbur et al., 2012; Hanslmayr et al., 2008; Jiang et al., 2015), intersensory conflict (Marly et al., 2023; Morís Fernández et al., 2015, 2018), and instances following incorrect responses (Cavanagh et al., 2009; Narayanan et al., 2013) or negative feedback (Marco-Pallares et al., 2008). Additionally, although heightened MFT activity is observed in common motor-conflict paradigms (Cohen & Donner, 2013; Jiang et al., 2015; Haciahmet et al., 2021; Drew et al., 2022), it is not limited to such situations. Studies focusing on stimulus-stimulus conflicts have employed protocols without response reports (Drew & Soto-Faraco, 2023) or with delayed response reports to mitigate motor contamination (Marly et al., 2023; Ruzzoli et al., 2020), while still observing an analogous pattern of increased MFT activity during conflict trials. In fact, recent research has challenged the strict functional and temporal demarcation between decision-making processes and motor actions. Instead, it suggests a parallel outlook of information processing, wherein the integration of evidence and the execution of motor outputs may coexist and interact (Cisek & Kalaska, 2010; McKinstry et al., 2008; Ozbagci et al., 2021; Resulaj et al., 2009). This notion aligns well with the observation of similar MFT variations in response to both purely perceptual-related conflicts and conflicts encompassing actions. For their part, value-biased decisions also exhibit resemblances to tasks commonly employed in cognitive control studies (e.g., Flanker, Stroop, Simon tasks), as choices bearing conflicting information are characterised by slower reaction times and increased error rates. This suggests that the conflict monitoring and control system, as revealed by frontal midline theta enhancement, may be integral to the detection of conflict between, and the resolution of the competition amongst, goal-relevant and value-based evidence for decision-making, thereby ensuring efficient performance.

Previous literature has typically employed the drift-diffusion model (DDM; (Ratcliff, 1978; Gold & Shadlen, 2007) to investigate the cognitive adaptations associated with value-based biases in decision-making processes. The DDM simulates decision-making

through the accumulation of noisy sensory evidence, referred to as the "decision variable," until a choice is finally made when it reaches a predefined threshold (or bound). This model has proven highly effective in predicting both choice accuracy and response times, shedding light on the underlying cognitive mechanisms involved in decision-making biases (Forstmann et al., 2016; Ratcliff & McKoon, 2008; Voss et al., 2004). The classical DDM can be adapted to account for the preference for one alternative over the other through the introduction of a "starting point bias." This bias initially shifts the accumulation of evidence towards the favoured alternative (Summerfield & Koechlin, 2010; Mulder et al., 2012; Voss et al., 2004; Mochol et al., 2021). Another common extension of the DDM explains how differential reward outcomes bias perceptual decisions by incorporating a "drift bias," which accelerates the accumulation of evidence toward the preferred option (Afacan-Seref et al., 2018; Fan et al., 2018). More sophisticated mechanisms have also been introduced to account for perceptual decisions with asymmetric rewards (Diederich, 2008; Diederich & Busemeyer, 2006; Shinn, Ehrlich, et al., 2020) but in all cases, the outcome associated with each response was artificially manipulated and known before the onset of the choice alternatives or target. Consequently, participants were able to adapt their evidence accumulation based on these response-reward contingencies (Corbett et al., 2023; Noorbaloochi et al., 2015; Blangero & Kelly, 2017). Hence, it remains unknown whether value can influence decisions when response-reward contingencies are not known in advance, and the mechanisms through which decision processes may be biased. Although cognitive control has been proposed to play a role in adjusting the decision-making processes towards goal-relevant evidence, as far as we know there is currently a lack of research investigating the connection between conflictrelated mid-frontal theta oscillations and value-biased decisionmaking processes.

In the present study, we introduce a novel experimental paradigm that combines a decision-making task with scalp EEG recordings to address the role of cognitive control in regulating decision making towards the goal-relevant evidence in the light of conflicting subjective value. To do so, we set out to address the following questions: (a) We investigate whether task-irrelevant preferences exert a bias on choice decisions regarding task-relevant attributes when both attributes are available concomitantly. We employ edible items, characterised by subjective values and objectively estimated prices. If this bias exists, we anticipate two primary outcomes. Firstly, if value biases depend on the fast and automatic activation of the VBS, we expect choices to be equally biased regardless of the amount of task-relevant information available (choice difficulty) which is integrated later in the decision process. Secondly, we predict that faster decisions will be more significantly affected by value than slower decisions, indicating the presence of a timedependent correction mechanism. Additionally, while edible items possess the inherent advantage of naturally encapsulating intrinsic preferences and prices, how one attribute relates to the other at an individual level cannot be experimentally manipulated and may impose some challenges. One we anticipated is that, for certain participants, the estimated prices and subjective values of items may exhibit a positive correlation, giving rise to what we term a "preference-for-expensive bias". This bias could potentially arise from the well-established association between the prices of goods and their perceived quality (Rao & Monroe, 1989). If such relation exists, we predict it may have the counter expected effects of value on choice behaviour, with a propensity to select the non-preferred, typically cheaper, alternative. (b) By examining variations in frontal midline theta activity, we aim to explore whether the cognitive control network is involved in regulating decisions towards taskrelevant evidence. We hypothesize that this network plays a role in detecting and potentially resolving conflicts between automatic activation of subjective value-based representations and objective task-relevant information to be used for correct choice. Lastly, (c) we aim to investigate whether intrinsic preference biases in objective decisions can be modelled using the classical DDM framework and identify the mechanisms at play.

Methods

The experimental paradigm, inclusion criteria and main analyses were pre-registered and are available here: <u>https://osf.io/msdzx</u>.

Experimental task and design

We developed a novel experimental design divided in three phases. First, a stimulus selection phase where participants were presented with 236 products of food and drinks typically available in supermarkets in Spain. Their task was to reject products they didn't recognise or for which they didn't have any idea of the taste. Participants had no time limit. Rejected products were removed from the subsequent phases. In case less than 180 products were selected, the participant was discarded. In the second phase (Figure 1 - left), participants were asked to rate the previously selected products on two parameters: the subjective value of that foodstuff, and its objective monetary price. For subjective value estimation, participants rated how much they like the product presented (by mouse clicking on a visual scale from -100 to 100 with a single tick-mark in the middle), they were encouraged to sometimes think of the products cooked or as part of a meal and to dissociate the frequency at which they consume the product from the pleasure they feel consuming it. During the rating of the objective price, participants had to estimate the monetary cost of the product in a supermarket (visual scale bar from 0 to 10 euros). To encourage precision of participants estimations, the three last rated items were displayed on the visual scale bar. Subjective value and price rating were self-paced, included several breaks, were run in separate blocks, and were presented in a random order between participants.

The third (and last) phase consisted of the experimental choice task of interest (Figure 1 - right), where in addition to behaviour, neural data was recorded using scalp EEG. Participants were introduced with a realistic context in which they had to go grocery shopping in the supermarket. They were asked to fill up 16 shopping carts (separate experiment runs) composed, each of them, of 80 products with the goal to fill the shopping carts as cheap as possible. To do so, they were presented with pairs of products, and they quickly had to select (one second time limit) the cheapest product. Each trial started with a fixation cross presented for 1200ms, a pair of items was then presented on the screen and disappeared as soon as a response was made or after 1100ms. The items were presented as square images (8x8cm) in the centre of the screen separated by a small space (2cm) with a fixation cross in the middle to limit eve movement. The selected item was added to participants' virtual shopping carts. If no response was made on time, the most expensive product was automatically added and participants were presented with the feedback message 'you were too slow, try to be faster' for 3 seconds. To incentivise good performance, participants were told they would win a product (randomly selected) from each shopping cart whose cost was less than 15 euros above the optimal (cheapest possible) one. Participants received their item(s) right at the end of the experiment. Their performance was displayed at the end of each run

Before starting, participants were presented with two mini shopping carts (20 trials each) to practice the task and get acquainted with the experiment pace and response deadline. These practice runs were not considered for analysis. Breaks were offered to participants in the middle and in-between each run.

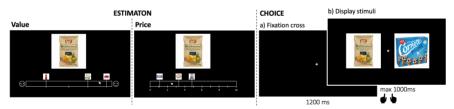


Figure 1. Experimental design. **Estimation**: Participants estimate the value (preference) or prices of all recognised items by clicking on the bar. The three last estimated items are displayed on the bar to facilitate participants' ratings. **Choice**: trial sequence. Participants quickly select the cheapest item using button presses. The items disappear as soon as they answer or after 1100ms.

Experimental conditions

During the experimental choice phase, participants were presented with pairs of products which varied in price difference (from 0 to 3 euros) and in subjective value difference (from 0 to 60, arbitrary rating scale units). The directions of the differences in price and values between the two products characterised the congruency condition. Among pairs with large subjective value difference ($40 \le \Delta V \le 60$), half were defined as congruent (C+) because the preferred item was also the cheapest (and hence the correct choice), and the other half were defined as incongruent (C-) because the preferred item was the most expensive (and hence, incorrect choice). Pairs with a small value difference ($\Delta V \le 20$) were defined as carrying no congruency (C₀).

The item pairs were selected online during the experiment, based on the individual ratings from the first two phases. The selection used a custom-made algorithm which maximised the number of positively rated (value) products included and homogenised pairs over the different conditions: difference in price between the pairs of items and congruency. The goal of the algorithm was that participants were presented with around 75% of trials with a congruency component (half C+ and half C-) and 25% of trials with no congruency component (C₀). Given the variable nature of subject's ratings, this ideal distribution of trials could not always be achieved but the proportion of congruent and incongruent trials was always kept equal.

To homogenise the materials included in the final analyses, we filtered out a posteriori trials containing items with negative subjective ratings (disliked) and trials with intermediate value difference ($20 \le \Delta V < 40$), to ensure a sufficiently strong congruency manipulation. To be clear, these trials were included in the experiment but not analysed as part of our hypothesis testing. We also excluded trials for which the reaction time was faster than the individual mean minus 3 standard deviations, as they were considered premature responses. These screenings were preregistered and applied before any data analyses. They resulted in less than 15% of trials rejected on average per subject. Mean percentages and numbers of trials included in the analyses for each experimental condition are displayed in Table S1.

In practice, trials with no-congruency (C₀) show an average subjective value difference (±standard deviation (s.d.)) of 4.81 ± 0.46 . As expected, no congruency effect between value and price was present for this subset of trials in any of our measures of interest: accuracy, z = .62, p = .54; RT: z = .11, p = .91; theta power: $\chi_1^2 = .055$, p = .81. Please note that trials considered as carrying a congruency (C+ and C-) had an average subjective value difference of 49.28±0.75.

As pre-registered, the price difference condition (ΔP) was discretized in three bins, small (between 0 and 1 euro), medium (between 1 and 2 euros) and large (between 2 and 3 euros) for data visualisation.

Participants

Participants were recruited from the Centre from Brain and Cognition (CBC) database based on several criteria. We followed the following in/exclusion criteria. First, participants who follow any specific diet (e.g., vegetarian, vegan, etc) were excluded, in order to maximize the number of liked edible products. Second, we only selected participants who had lived in Spain for at least the past year, to maximize product familiarity and knowledge of prices. Participants ages were between 19 and 34 years old, and they were excluded if they were presently undergoing psychological conditions or medical treatment. Finally, participants were asked to fast during the 3 hours preceding the experiment, as we reasoned this would make liked products more appealing. The whole experiment lasted between two and three hours in total and participants received 5€ compensation per half hour spent in the laboratory (a total between 20 and 30 euros). Additionally, participants whose performance was good enough (within 15euros of the theoretical optimal cart) received a real product randomly selected from their virtual shopping cart (16 out of 34 participants left the laboratory with a minimum of one and up to sixteen products). After completion of the experiment and before data analysis, we applied additional pre-established exclusion criteria. We excluded participants with less than 10 valid trials per experimental condition (congruency x ΔP x Reaction time (median split)) for the behavioural analyses, and 20 trials for the EEG analyses. We also excluded participants for which the price difference (ΔP) was significantly different between the congruent and incongruent conditions to have balanced conditions. Finally, we removed participants for whom the proportion of correct trials was not significantly higher than chance.

According to the pre-registration, recruitment continued until the completion of a sample size of 30 valid datasets (30 meeting the behavioural performance and EEG criteria, and 1 meeting only the behavioural criteria). The final sample size includes 31 participants for the behavioural analyses (16 females, mean age \pm s.d.: 23.3 \pm 3.8 years old) and, out of those, 30 for the EEG analyses (15 females, mean age \pm s.d.: 23.3 \pm 3.8). Among the thirty-four participants initially recruited, three were excluded from all analyses based on the pre-established criteria that price difference in congruent and incongruent trials shouldn't be significantly different. One additional participant was excluded from the EEG analyses because of an insufficient number of trials per condition.

EEG recordings

Data was recorded using a 64-electrodes EEG system mounted in a standard (10–10 international system) ActiCAP (Brain Products GmbH, Munich, Germany) and the signal was recorded via BrainVision Recorder (Brain Products GmbH, Munich, Germany) at a sampling rate of 500 Hz. The online reference was placed on the right mastoid and the ground electrode on AFz. Eye movements were captured with two electrodes (Veog and Heog) respectively placed underneath and at the outer canthus of the right eye. Impedance was lowered below 10 k Ω for all electrodes.

EEG pre-processing

EEG data was pre-processed and analysed with Fieldtrip (Oostenveld et al., 2010) using custom code in MATLAB (2022b). We first removed excessively noisy and faulty electrodes (1 electrode was removed for 6 participants and 2 electrodes were removed for 3 participants). Data was segmented in trials starting at fixation onset and ending 500ms after the stimuli disappearance and filtered using a dual-pass Butterworth filter with a passband of 0.1-50Hz (order 2) and a notch filter of 50Hz. Overlaps in the data were then removed to apply an independent component analysis (ICA). Using components head maps and spectral components, one to two independents component were manually removed per participant (mean: 1.17), corresponding to blinks and horizontal eve movements. Data was then manually inspected to remove the remaining artefacts. Finally, data was re-referenced to average of all scalp electrodes and missing channels were interpolated using spherical splines (Perrin et al., 1989).

Analyses

Behavioural data was analysed using R and MATLAB. To use consistent statistical approaches for behavioural and neural data we chose to use mixed effect models (MEM). The significance of each factor or interaction of interest predicting accuracy, RT and MFT power was evaluated using forward model selections based on likelihood tests ratio and all steps are reported (see Tables S2 to S7). When outliers were detected (more than 1.5 interquartile range [IQR] away from the distribution mean), correlations were run both including and excluding the outliers. Multiple comparisons were always corrected using the Bonferroni method. Sizes of congruency effects (comparing C+ and C- trials) on our main variables of interest were calculated using Cohen's *d*.

Choice behavioural analysis

Accuracy, defined as the probability to select the cheapest item, was analysed using generalized linear mixed-effect models (GLMM) while reaction time (RT) was log-transformed and analysed using linear mixed-effect models (LMM). In both cases, subjects were introduced as random intercepts. We used the ascending method to test the effect of the factors of interest. RT analyses used only correct trials, unless specified. As expected, we did not find significant interactions between congruency conditions and price difference (ΔP). To further assess if this negative result could be due to a lack a power, we ran a posteriori sensitivity analyses to estimate the minimum effect size that could have been detected with powers of at least 80 and 95% using the R package *simr* (Green & MacLeod, 2016).

EEG Time-Frequency Analysis

As we found differences in response speed between experimental conditions, we analysed the EEG data response locked (as mentioned in the pre-registration). The EEG analysis focused on oscillatory activity in the theta range (4-7Hz), therefore, to get a reliable estimate of theta power, we used a sliding window of 500ms on our defined epoch. Time frequency analysis was performed using short-time Fourier transform (STFT) in steps of 20ms with a single tapper (Hanning). Missed trials (no response) and trials with a RT inferior to 500ms were excluded from the analysis leaving on average (\pm s.d.) 92.1 \pm 6.8% of the included trials. Before analysing, we applied the spherical splines method (Perrin et al., 1989) to increase spatial resolution.

For completeness, time-frequency analysis of MFT stimulus-locked is briefly presented in the supplementary results (Figure S5).

Single Trial EEG Analysis

Based on the time frequency analyses of congruent and incongruent trials, we defined a 500ms window of interest from -450 to 50ms relative to the response. The effect of the experimental conditions (congruency and price difference) on mid-frontal theta (MFT) power were tested using LMM with subjects as random intercepts. MFT power has previously been found to correlate with response time and performance accuracy (Cohen & Donner, 2013). To explore these relations, we tested the significance of MFT as a

predictor of accuracy and RT using GLMM (binomial) and LMM respectively, both with subjects as random intercepts and slopes.

Motor-related EEG correlates

Motor preparation for response was analysed through interhemispheric imbalances in parietal beta-band (13-30Hz) desynchronization, and lateralized-readiness potential (LRP). Beta oscillations were averaged over the electrodes C1, C3, C5, CP3, FC3 (left) and C2, C4, C6, CP4, FC4 (right) and contrasted as a function of response side (contralateral minus ipsilateral to response hand). Beta oscillations were estimated using a similar approach as for MFT oscillations. LRP was calculated as the difference between the ipsilateral vs. contralateral activity of electrodes C3 (left) and C4 (right) and an additional Butterworth lowpass filter at 4Hz was applied prior to analyses. Both correlates were analysed stimulus and response-locked, and baselined with the 500ms time window prior to stimulus onset.

Modelling the response behaviour

We modelled participants reaction time (RT) and accuracy at the binary choice task using drift-diffusion models (DDM). The DDM assumes that decisions are made through a noisy process that continuously accumulates evidence over time, represented by a decision variable x, until it reaches one of the two decision boundaries (see Figure 9). These boundaries correspond to the amount of evidence required to make a decision. In an unbiased choice, the starting point of the accumulation process x_0 is situated at the midpoint of the two bounds. The drift rate μ in the DDM represents the strength or quality of the evidence supporting each decision alternative. It determines the direction and speed at which evidence accumulates over time. Higher drift rates indicate faster and more accurate decision-making, while lower drift rates indicate slower and less accurate decision-making. The choice reaction time is set to be the sum of the decision time formalised in the DDM process, and a non-decision time, which accounts for afferent and efferent delays unrelated to the decision itself, such as stimulus encoding, motor preparation, or response execution. Lastly, the DDM incorporates the amount of noise or random variability in the evidence accumulation process. It is modelled here as a Wiener process (i.e., a sample from a Gaussian distribution with mean 0 and variance 1). The parameters of the fitted models are summarised in Table 1. and described in more detail below.

Modelling urgency

We observed in our data that slower choices are not necessary associated with higher accuracy, suggesting the presence of an urgency signal. These results are not surprising, given the time pressure imposed by the short response deadline (one second). To capture this urgency signal, we employed a linear "gain function", that uniformly scales both evidence and noise uniformly throughout the course of the trial (Cisek et al., 2009; Ditterich, 2006). We also attempted to model the urgency signal using "collapsing bounds", where the decision bounds decayed linearly or exponentially with time. This manipulation causes the decision bounds to become more permissive as the trial progresses (Drugowitsch et al., 2012; Shinn, Ehrlich, et al., 2020). We found that our data was better fitted (measured using Bayesian Information Criterion – BIC) using a linear gain function compared to collapsing bounds. As a result, we report only models that include an urgency signal u(t) modelled as follows.

$$u(t) = \sigma_0 + s_u \bullet t$$

where σ_0 represents the urgency at time t = 0, and s_u the slope of the linear ramp in gain function with time t. The bounds are constant over time and fixed at B(t) = 1.

Notation	Definition
Task variables	
ΔP	estimated price difference between the two alternatives
С	congruency, 1=congruent; -1=incongruent
Parameters	
μ	Drift rate ($\mu \ge 0$)
x_0	Starting position of the decision variable $(x_0 \in \mathbb{R})$
σ_0	Urgency at time $t = 0$ ($\sigma_0 > 0$)
m_{nd}	Mean of gaussian distributed non-decision time ($m_{nd}\geq 0$)
σ_{nd}	Standard deviation of gaussian distributed non-decision time ($\sigma_{nd}>0$)
p_L	Probability of a lapse ($p_L \ge 0$)
s _u	Slope of linear ramp in gain function ($s_u \in \mathbb{R}$)
t_D	Onset time of integration of goal relevant evidence
d_B	Drift rate biased towards either the preferred or non-preferred item ($d_B \in \mathbb{R})$
p_{map}	Probability of a mapping error given the threshold was crossed ($p_{map} \geq 0$)
ł	Leak magnitude, $0=$ perfect integration; $\infty=$ no integration ($\ell\geq 0$)
Miscellaneous	
x	Decision variable
B(t)	Decision bound
u(t)	Gain function
W	Wiener process
Ι	Indicator function

Table 1. Mathematical annotations used in the DDMs. [back to Results]

Modelling non-decision time

Non-decision time was first modelled as fixed value for each participant or drawn from a posterior distribution (uniform or gaussian) which enabled trial-by-trial variation. We observed that using a gaussian distribution of the non-decision time was predicting the data the best.

 $t_{nd} \sim N(m_{nd}, \sigma_{nd})$

where the non-decision time t_{nd} is drawn from a normal distribution with mean m_{nd} and standard deviation σ_{nd} .

Additionally, in order to be able to predict contaminant responses (for example, very fast responses), we implemented a mixture model where the probability of a lapse trial p_L is drawn from a uniform distribution U(.001,.2).

Modelling value biases

We observed that participants preference for one of the two presented items biased both their reaction times and responses accuracy. The effect on RT was consistent and resulted in preferred items (higher estimated value of the pair) being chosen faster than the non-preferred ones, both for correct and incorrect choices. The effect of value on choice accuracy was less consistent as it varied with participants RT. Overall, we observed higher accuracy for congruent trials, where the correct alternative was also the preferred one, compared to incongruent trials for the faster responses (median split on the RT), while the opposite was true for slower responses. To model such effects, we started by implementing simple biases affecting the accumulation process.

Starting point bias

First, we introduced a starting point bias x_B which bias the initial point of the accumulation process towards one of the alternatives; the preferred one (correct response in congruent trial, or incorrect response in incongruent trials) or the non-preferred one.

 $x_0 = x_B \bullet C$

The initial point x_0 of the decision variable is biased symmetrically in congruent (C = 1) and incongruent trials (C = -1). This bias has been shown to explain value-biased decisions (Summerfield & Koechlin, 2010; Mulder et al., 2012). However, in our task, the reward-response contingencies (position of the preferred alternative) are not known before the stimuli onset which differ from previous studies. This led us to suppose that the value bias may not affect the starting point of the evidence accumulation but rather the integration of evidence with time.

Drift rate bias

As a result, we introduced an additional drift rate biased toward either the preferred or the non-preferred alternative d_B . Similar to the starting point bias, the drift rate is biased symmetrically in congruent (C = 1) and incongruent trials (C = -1).

As we didn't have a priori hypothesis regarding the interaction of a potential drift bias and the urgency signal we modeled it both individually (1) and interacting with the gain function u(t) (2):

(1)
$$dx = \mu \bullet \Delta P \bullet u(t) \bullet dt + u(t) \bullet dW + d_B \bullet C \bullet dt$$

(2)
$$dx = (\mu \bullet \Delta P + d_R \bullet C) \bullet u(t) \bullet dt + u(t) \bullet dW$$

Hypothesis driven biases

Using both the drift rate and starting point biases, we were not capable to reproduce the value biases observed in behaviour, therefore we introduced more complex mechanisms based on the hypotheses we had regarding the underlying cognitive mechanisms at play. First, based on the idea that value-based evidence may be integrated first in the decision process while the goal-relevant information is taken into account later, we introduced a decision variable:

$$dx = I_{t \le t_D} (d_B \bullet C \bullet dt) + I_{t > t_D} (\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$$

where evidence related to the price difference (ΔP) is only integrated after a delay t_D . This model resembles the idea of *two*stages hypothesis where the different attributes of the stimuli (here subjective value and price) are considered sequentially (Diederich, 1997, 2008).

Following our hypothesis based on previous studies that value affect the decision early-on and fades as the decision unfolds (Afacan-Seref et al., 2018; Noorbaloochi et al., 2015; Summerfield & Koechlin, 2010), we considered a drift bias which decreases with time exponentially:

$$dx = \mu \bullet \Delta P \bullet u(t) \bullet dt + u(t) \bullet dW + (d_B \bullet C)/(t+1) \bullet dt$$

or linearly:

$$dx = \mu \bullet \Delta P \bullet u(t) \bullet dt + u(t) \bullet dW + (d_B \bullet C - t) \bullet dt$$

Finally, as an attempt to model the unexpected effect of value observed on slower choices, with congruent trials being less accurate than incongruent trials, we introduce a drift bias which increases with time:

$$dx = \mu \bullet \Delta P \bullet u(t) \bullet dt + u(t) \bullet dW - d_B \bullet C \bullet t \bullet dt$$

As the decrease in accuracy with time is only observed for congruent trials but not for incongruent trials, we also implemented a late drift bias which affects only congruent trials (C = 1) and is null for incongruent trials (C = 0):

$$dx = \mu \bullet \Delta P \bullet u(t) \bullet dt + u(t) \bullet dW - d_B \bullet C_{+} \bullet t \bullet dt$$

Modelling errors

We observe that models were predicting a probability of correct choices superior to the one observed in the data, for both congruent and incongruent trials, so we intended to lower the predicted accuracy using two mechanisms. First, we considered the possibility that participants do not integrate the evidence perfectly over time by introducing a leak term ℓ (Cisek et al., 2009). We observed that this leak term could not explain the probability of errors observed in the data.

Secondly, we considered a mechanism unrelated to the integration process which traduces an error in mapping between the evidence accumulation and the generation of the motor response (Shinn, Ehrlich, et al., 2020; Hanks et al., 2015; Erlich et al., 2015). We modelled this mapping error to occur, with a certain probability p_{map} , once the decision variable had reached the bound associated with the correct, cheapest alternative, and to bias participants to mistakenly generate a motor response towards the incorrect, more expensive alternative instead. This mapping error was implemented by modifying the simulated distribution of reaction times. For a simulated probability density function f(x | R), where R is the

response accuracy; correct or incorrect, we computed the final density f'(x) using f'(x), calculated as follows:

$$f'(x \mid R = err) = f(x \mid R = err) + p_{map} f(x \mid R = corr)$$
$$f'(x \mid R = corr) = (1 - p_{map}) f(x \mid R = corr)$$

We thought that, due to the strict response deadline imposed to participant, such error in mapping could be plausible.

Model fitting

Fitting the model to the data and simulations were performed using the PvDDM package in Python (Shinn, Lam, et al., 2020) with a time step of 5 ms and decision variable discretization of 0.005. The python code and notations of the different model parameters used were adapted from (Shinn, Ehrlich, et al., 2020). The data was fitted for each participant individually and separately for trials carrying a congruency component (large ΔV , congruent and incongruent trials) and no congruency (small ΔV). Such distinction was made first to understand the mechanisms underlying the value-biases observed and, seeing the difficulties encountered to reproduce our data (see Results), to see whether trials a priori not biased by value could be explained using the DDM. Goodness of fits were estimated using the Bayesian Information Criterion (BIC) and the best predicting model was assessed by comparing the averaged BIC over the participants. All models had at least 6 free parameters: a drift rate μ , two urgency-related parameters σ_0 and s_u , two parameters related to the non-decision time m_{nd} and σ_{nd} , and p_L predicting the rate of lapse trials.

Results

Estimated prices and preferences

First, we assessed the quality of participants' price estimations by examining the correlation with actual supermarket prices for all participants (Kendall's correlations, all p < .001). Regarding value ratings, they were predominantly positive (80.4%) and we observed

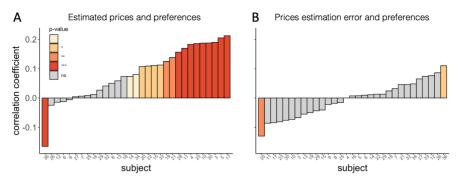


Figure 2. Half of the participants tend to prefer more expensive items, whereas only one did show a correlation in the reverse direction. Results of individual correlations between price and preference estimations (A) and between price estimation error (difference between real and estimated prices) and preferences (B). Individual coefficients (tau) extracted from Kendal correlations are ordered by magnitude. Colours represent the significance levels ('ns': $p \ge .1$, '.': p < .05; '**': p < .01, '***': p < .001).

that for approximately half of participants value ratings were positively correlated with price estimations (Figure 2A). For these participants, then, there was a preference for more expensive items: the preference-for-expensive bias. However, except for two participants, we didn't find any correlation between the error in price estimation and subjective value ratings (Figure 2B) suggesting that participants do not systematically over or underestimate the items they like and are able to give objective estimations of the items' prices. The preference-for-expensive bias was anticipated (see pre-registration). Indeed, the association between the price of goods and their perceived quality is well established (Rao & Monroe, 1989), providing a potential explanation for the observed phenomenon. For instance, studies have demonstrated that elevating the price of a wine is linked to heightened subjective reports of pleasantness (Plassmann et al., 2008). Hence, the preference-forexpensive bias potentially exists within all individuals; however, within the context of our subset of edible items, it becomes statistically evident only among a specific subgroup of participants. Here we assumed that, if this bias has any impact, it would be in the opposite direction of the congruency bias of interest in our study. That is, the congruency bias of interest would make participants chose preferred items more often and rapidly, whilst in our dataset

participants who tend to prefer more expensive items should in fact be more inclined to show the opposite bias. Indeed, they should tend to direct their choice toward the usually cheaper, non-preferred item, thus excluding the possibility of a confound leading to a false positive.

Subjective preference exerts a bias on objective choice behaviour

Choice accuracy in the main task was analysed using generalized mixed effect models (GLMM), with subjects as a random variable (see Table S2). Model selection revealed a significant effect of congruency between value and price (model m_1), with congruent trials being more accurate than both incongruent and no-congruency trials (see Table S3 for statistics). A main effect of price difference was also found (model m_2) with accuracy increasing with ΔP , and a main effect of RT (model m_3) with longer RTs being associated with lower accuracy. No significant interaction was found between price difference and congruency (model m_4 , Figure S2A) suggesting, as anticipated, that the observed congruency effect is due to an early automatic influence of value preceding a voluntary choice strategy. To further assess the absence of interaction, we run sensitivity analyses estimating the minimum effect sizes that could have been detected between the congruency conditions (here C+ or C- only) and ΔP . We found that effects of $\pm .15$ and $\pm .18$ could have been detected with powers of 87.33% (95%CI = [80.9, 92.2]) and 98.7% (95%CI = [95.3, 99.8]) respectively. In comparison, the interaction between congruency and RT revealed a fixed effect of .46. Therefore, if the congruency effect in choice behaviour were a deliberate strategy, one would anticipate its strength to diminish with ΔP . If such reduction exists, it seems to be relatively minor, as it would have been otherwise detected in our experiment. Finally, as previously reported in the literature, a significant interaction between congruency and RT was found (model m_5). The interaction can be explained by the following patterns. First, accuracy decreases with increasing RT, and this decrease is more pronounced for congruent trials compared to both incongruent and nocongruency trials, and for no-congruency trials compared to

incongruent trials (Table S3 and Figure S1). Second, the magnitude of the congruency effect is larger for faster RTs (Figure 3A) (comparing the observed accuracy in fast C+ and C- trials: V = 385, $p_{adj} = .012$, Cohen's d [95% CI] = .53 [.01, 1.08]), an expected and well-known effect in the literature of value-biased decisions (Summerfield & Koechlin, 2010; Afacan-Seref et al., 2018; Noorbaloochi et al., 2015). However, in our data we additionally observed a complete reversal of the congruence effect at longer RTs, with congruent trials which tended to be responded to less accurately than incongruent trials (V = 145, $p_{adj} = .087$, Cohen's d [95% CI] = -.56 [-1.05, -.05]). This effect was not expected and is discussed in the next section.

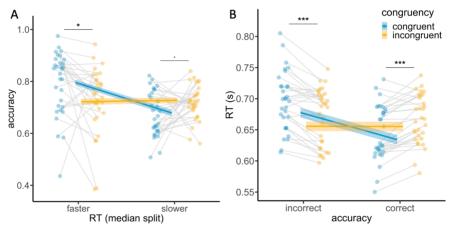


Figure 3. Participants' preferences affects both accuracy and reaction times (RT). Lines represent the predicted mean accuracy (A) and RT (B) using mixed effect models. Shaded areas represent the standard error of the mean (s.e.m.). Individual observed data is plotted (colour dots) for each congruency condition and linked with grey lines. Results of post-hoc comparisons between congruent and incongruent observed data inside each condition are displayed according to adjusted p-values ('.': $p_{adj} < .1$; '*': $p_{adj} < .05$; '***': $p_{adj} < .001$).

Log-transformed RTs were analysed with linear mixed-effect models (LMM) including both correct and incorrect trials to gauge the potential interaction between accuracy and congruency (Noorbaloochi et al., 2015). Indeed, model selection revealed this interaction as significant (<u>Table S4</u> – model m_4); for correctly responded trials congruent ones were faster than incongruent ones (comparing the observed RTs: $t_{30} = -6.06$, $p_{adi} = 2.4 \times 10^{-6}$, Cohen's d [95% CI] = -1.09 [-1.74, -.70]), whereas for incorrect responses congruent trials were slower than incongruent ones $(V = 461, p_{adi} = 8.0 \times 10^{-6}, \text{ Cohen's } d \text{ [95\% CI]} = 1.07 \text{ [.72,}$ 1.59]) (Figure 3B and Table S5). Overall, this pattern reflects that when participants chose faster, they tended to choose the item they preferred. Again, we did not find any interaction between congruency and price difference (model m_5 , Figure S2B), nor a 3way interaction with accuracy (model m_7). However, as expected, we found a significant overall effect of price difference on RTs (<u>Table S4</u> – model m_3), with participants responding faster to trials with larger ΔP . In accordance with the effect of price difference found on accuracy, these results suggest that price difference between the two alternatives modulates difficulty; the larger ΔP the easier the trial (leading to more accurate and faster responses). Mirroring our approach with accuracy, we performed an a posteriori sensitivity analysis to estimate the minimum detectable interaction between congruency (C+ and C- only) and ΔP . Results revealed that effects of $\pm .015$ and $\pm .02$ could have been detected with powers of 82.2% (95%CI = [79.7, 84.5]) and 97.5% (95%CI = [96.3, 98.4]) respectively. In comparison, the interaction between congruency and response accuracy demonstrated a fixed effect of .065. Therefore, results show that if the influence of subjective value on RT is indeed modulated by ΔP , it appears to be relatively modest in magnitude, as a more substantial effect would likely have been detected. Together with the analyses of response accuracy, these findings suggest that the items' value has an automatic effect on choice behaviour, seemingly independently of the amount of taskrelevant evidence available.

Finally, we investigated whether the influence of preferences on both response choices and response times was modulated by participants experience at the task. Accuracy was analysed using a GLMM, incorporating congruency, response time (median split), and time-on-task (run 1 through to 16, corresponding to the sixteen presented shopping carts) as factors (Figure S3A). We observed a significant main effect of time-on-task, indicating that participants became more accurate as the experiment progressed $(\chi_1^2 = 31.61, p = 1.88 \times 10^{-8})$. Additionally, a significant interaction between congruency and time-on-task was observed $(\chi_1^2 = 9.21, p = .0024)$, indicating a stronger improvement in accuracy for incongruent trials compared to congruent trials resulting in choices being less biased by value as time unfolded in the experiment. Regarding response times, we employed the same methodology and used mixed-effects models to examine the relationship between response time, and congruency, response accuracy, and time-on-task (Figure S3B). The results revealed a decrease in response time with time-on-task $(\chi_1^2 = 300.38, p < 2 \times 10^{-16})$. However, contrary to the findings in accuracy, no interaction between congruency and time-on-task was observed ($\chi_1^2 = .016$, p = .90). Taken together, these findings demonstrate that participants became both more accurate and faster as they progressed through the task. They indicate that while value biases in response time persist throughout the experiment, the tendency to quickly select the preferred alternative diminishes over time, and that when responding slower, the inclination to select the least preferred alternative more frequently increases with time-ontask. These results suggest that subjective value biases in response choices are dependent on participants' familiarity with the task, whereas the value biases observed in response times likely rely on more automatic mechanisms and remain unchanged regardless of participants' experience.

The interaction between subjective value and price is a source of choice behaviour variability

Overall, the results so far suggest that fast decision-making is biased by the automatic integration of task-irrelevant value-based preferences, resulting in more frequent selection of preferred items regardless of the magnitude of the objective task-relevant evidence (ΔP). However, an apparently atypical finding was that, for slower choices, accuracy in congruent trials was lower than in incongruent trials. We hypothesised that this unexpected effect might be a consequence of the positive correlation between price and preference, significant for 15 out of 31 participants in our dataset (Figure 2A). For this group of participants, preferred items are consistently associated with higher prices and therefore to the incorrect response in congruent trials. This association may have induced a response adaptation during the experiment that influenced a choice strategy in favour of the non-preferred option, since in their case it is, more frequently than not, the correct answer. To support this account, we conducted exploratory analyses. First, we ran correlation tests between participants' accuracy and the magnitude of their individual price-preference correlation coefficient. This correlation tests were run for each congruency condition separately. If the account above is correct, the error rates on congruent trials should scale with the participants' price-preference correlation strength. Indeed, we observed a significant negative correlation between accuracy and individual price-preference correlation strength, only within congruent trials (Figure 4A, Pearson, r = -.50, p = .005; incongruent trials, Spearman, r = .03, p = .88).

Additionally, we re-run the initial analyses on accuracy and RTs separately for those participants that showed a significant preference-for-expensive bias and those that did not (threshold p=.05, Figure 4B). For the latter group (no positive preference-price correlation), we observed a significant effect of congruency within faster trials ($V_{16} = 8, p_{adj} = .003$) and not on slow responses $(V_{16} = 65, p_{adi} = 1)$, which was in principle the expected pattern. However, and confirming our post-hoc explanation, for the group with a significant positive price-preference correlation we found an overall bias toward the non-preferred items, leading to lack of congruence effect for fast responses $(V_{15} = 55, p_{adi} = 1)$ and the atypical reversal of the congruence effect in slower trials $(V_{15} = 106, p_{adi} = .027)$. Therefore, the pattern of congruency effects observed is, at least in part, modulated by participants' strength of association between subjective value (preference) and price: in participants with a strong positive association, their behaviour is biased towards choosing the least preferred but, consistent with their prior, most likely cheaper (correct) option.

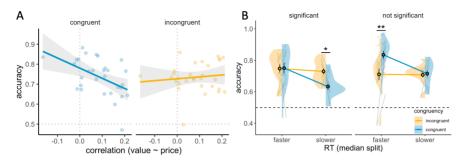


Figure 4. Accuracy is differentially affected by preference depending on participants' prior relation between prices and values of the eatable items. A. Participants' accuracy depending on their correlation coefficient between estimated prices and preferences. Each dot represents a participant, the line corresponds to the linear regression and the grey shaded area its 95% CI. B. Distributions of accuracies depending on trial reaction time (median split), congruency and participants positive correlation between estimated prices and preferences (significant or not, for p < .05 and r > 0). Coloured lines connect distributions averages and black error bars represent their s.e.m. Grey lines connect individual data. Results of post-hoc comparisons are displayed according to adjusted pvalues ('**': p < .01, '***': p < .001). Samples sizes per condition: 'significant': n=15, 'not significant': n=16.

We further investigated whether the strategy to choose the nonpreferred item is evident right from the outset of the experiment or whether it develops gradually as participants become familiar with the task. Employing similar analyses to those presented earlier (refers to Figure S3A), we modelled accuracy based on several factors: time-on-task (runs), congruency (C+, C-), and choice reaction time (median split on RT). However, in this instance, we introduced an additional factor to account for participants' preference-for-expensive biases (whether significant or not) (Figure S4). The results revealed a three-way interaction involving the presence of the preference-for-expensive bias, time-on-task, and congruency ($\chi_1^2 = 17.84$, p = 2.41 × 10⁻⁵). Post-hoc analyses unveiled a significant interaction between congruency and time-ontask among participants displaying a preference-for-expensive bias $(\chi_1^2 = 13.10, p = 2.96 \times 10^{-4})$, while no such interaction was observed among the remaining participants ($\chi_1^2 = .001, p = .97$). These outcomes suggest that the observed reduction in participants' inclination to rapidly choose the preferred alternative (as illustrated in Figure S3A) appears to stem from the existence, within a subset of participants, of a positive correlation between the estimated values of items and their prices. For these individuals, accuracy in congruent choices does not experience improvement as the task is carried out. This phenomenon may arise due to an adaptive mechanism that builds upon participants' prior expectation that the preferred items are generally more expensive. Conversely, participants who do not exhibit the preference-for-expensive bias witness an enhancement in accuracy for both congruent and incongruent trials over time, thus maintaining the unaltered impact of value on faster choices throughout the course of the task.

Lastly, based on previous literature predicting that prior expectation about stimulus probability has larger effect when the signal-to-noise ratio is low (Bogacz et al., 2006), we specifically tested whether the higher accuracy observed for incongruent compared to congruent trials was modulated by the task-relevant evidence (ΔP), in slower choices and for participants with a significant preference-forexpensive bias. No interaction between ΔP and congruency was found ($\chi_1^2 = 1.29 \text{ p} = .26$).

Contrary to participants' choices, response times were not related with individual correlations between estimated prices and preferences (Pearson's correlations, C-: r = .23, p = .23; C+: r = .33, p = .075), neither the magnitude of the congruency effect on RT (r = .30, p = .11), implying that RT are less sensible to participants priors than choices. These findings suggest that, although value may exert an automatic influence on choice behaviour that manifests as a consistent effect on RT, the preference-for-expensive bias might impact participants' decisionmaking process in a more deliberate manner, but still independently of the choice difficulty. This controlled influence could potentially account for the bias's exclusive impact on response choice.

Increased mid-frontal theta oscillations for conflictual subjective value and price.

We have demonstrated that, consistently with predictions, preferences affect participants' fast choices and RT, and this effect is independent on the amount of goal-relevant (price difference) information present. This suggests that value-based evidence kicks in early and possibly automatically, while the integration of objective task-relevant evidence (price) unfolds more slowly. We assume that the initial integration of value-based information is triggered by the VBS. In incongruent trials, later-arriving objective evidence about the correct choice contradicts the choice supported by subjective value. We hypothesised that this conflicting situation in incongruent trials would engage conflict-processing brain mechanisms, indexed via the amplitude of mid-frontal theta (MFT) oscillations in our experiment. To test this hypothesis, we analysed MFT power in a time window from 1200ms before stimulus onset until 500ms after the response (Figure 5). Overall, we observed a significant MFT increase after stimulus onset, and in each experimental condition separately (all p < .001). Firstly, we investigated whether the magnitude of this MFT increase is larger for price-preference incongruence, our principal question. As congruent and incongruent trials are characterised by different mean reaction times, we ran a time-resolved response-locked analysis (-1200 to 500ms, where t=0 is the response) for MFT power differences across congruency conditions (for completeness, stimulus-locked time-frequency analyses are reported in Figure S5). We found significantly higher MFT activity for incongruent compared to congruent trials during a 160ms window (-280 to -120ms) before response (Figure 5B, one-tail t-tests with Monte-Carlo multiple comparisons correction, t = 17.56, p = .047). We selected a window of 500ms centred around the peak of this significant difference to analyse MFT on a trial-by-trial basis using linear mixed effect models. Model selection revealed a significant effect of congruency (<u>Table S6</u>, model m_1), with higher MFT power for incongruent compared to congruent trials (Table S7 and Figure 5C, Cohen's d [95%CI] = .37 [.02, .73]) confirming the behavioural results, and the starting hypothesis that incongruent trials elicit a stronger engagement of conflict-related brain processes.

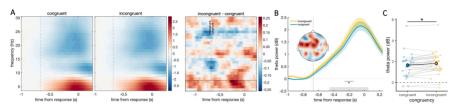


Figure 5. Incongruent trials are associated with higher mid-frontal theta power. A. Time-frequency analysis of congruent (left) and incongruent correct trials (middle) response-locked show an increase in theta power (dB) post-stimulus presentation. Difference between incongruent and congruent conditions (right) show a higher theta power before response. Vertical dashed lines represent mean stimulus onsets. **B.** Average mid-frontal theta power (4-7Hz) of congruent and incongruent correct trials plotted over time. A significant cluster was found from 260 to 140ms before response ('*': $p_{adj} < .05$) around which an analysis window was selected (grey shaded area: -450 to 50ms relative to response). The topographic head map represents the difference in theta power between incongruent and congruent trials over this analysis window. **C.** Average theta power predicted (Table S6 - m_1) for congruent and incongruent seem. Grey lines connect individual subjects (observed data). ('*': $p_{adj} < .05$).

As we have shown that the presence of the preference-for-expensive bias modulated the congruency effect observed on behaviour (see Figure 4), we addressed whether such bias also influenced the MFT (-450 to 50 relative to response) differently in congruent and incongruent trials. We conducted exploratory analyses and observed that participants' mean MFT activity was not affected by the magnitude of the preference-for-expensive bias (correlation coefficients between estimated prices and preferences) in either congruency condition (*Spearman's*, C-: r = -.17, p = .38; C+: r = -.17, p = .37; C₀: r = -.17, p = .38). Additionally, even though we found that MFT power is significantly higher in incongruent compared to congruent trials only for participants not showing a significant preference-for-expensive bias ($t_{14} = 2.31$, p = .037; significant bias: $t_{14} = 1$, p = .34, similar

results found with the time-frequency analysis in Figure S6A-B), the magnitude of this difference did not correlate with the bias magnitude (r = .066, p = .73, Figure S6C). These findings indicate that the preference-for-expensive bias had minimal or no influence on the extent of conflict-related MFT. While additional data is required to establish this potential interaction with greater certainty, the analyses presented in the subsequent section suggest that the preference-for-expensive bias affects the way MFT is relayed and impacts subsequent choice behaviour, rather than directly influencing the strength of MFT activity itself.

Mid-frontal theta oscillations account for individual variability in conflict detection.

Subsequently, we investigated whether the magnitude of MFT power estimated from the relevant 500ms time window (centred around the peak of the congruency effect), is associated with behaviour. Initially, we employed mixed effects models with MFT power as a single predictor, to explore its relationship with RT and accuracy in each congruency condition separately, allowing both the MFT power estimate and the intercept to vary for each subject. As previously, RT was log-transformed and fitted using a linear model while accuracy was fitted using a binomial logistic regression. Consistent with previous literature (Cohen & Donner, 2013), we found MFT power to be a positive predictor of RT in all congruency (C+: $t = 4.47, p = 1.34 \times 10^{-4}$; conditions C - : $t = 6.88, p = 4.12 \times 10^{-7}; C_0: t = 4.47, p = 1.34 \times 10^{-4}), and$ the strength of this relation did not significantly differ between conditions ($F_2 = 1.11, p = .33$).

MFT activity was a significant predictor of the response slowing observed in correct incongruent trials compared to congruent ones (r = -.42, p = .02), a behavioural effect which was consistent across participants (Figure 3B) and which was not modulated by individual preferences for expensive items, as opposed to subjective value biases observed on accuracy (Figure 4A-B). Additionally, the magnitude of the congruency effect on MFT (difference between C-

and C+) did not correlate with individual preference-for-expensive biases (Figure S6C). These results reveal that MFT sensitive to the value-price conflict is not correlated with behavioural biases triggered by participants preferences. In other words, the measured MFT may reflect the detection of conflict but not necessarily its resolution.

Regarding accuracy, we found that theta power was only a significant positive predictor of response accuracy in incongruent trials (Figure 6A, C+: z = .07, p = .95; C-: z = 2.28, p = .022; C_0 : z = .60, p = .55), with individual estimates being significantly higher compared to those for congruent trials $(t_{29} = -4.46, p_{adj} = 3.42 \times 10^{-4})$ and for no-congruency trials $(t_{29} = -4.75, p_{adj} = 1.53 \times 10^{-4})$. The difference between congruent and no-congruency trials was not significant $(t_{29} = -1.69, p_{adi} = .30)$. Together, these results suggest that higher cognitive control, as expressed through higher MFT power, is required to respond correctly in incongruent trials specifically. This confirms our hypothesis that, in incongruent trials, the competition between price and value-based evidence triggers a conflict (and possibly the ensuing mechanisms for its resolution). We assume then that the strength of the association between MFT and accuracy may serve as a proxy to investigate the presence of a conflict at the individual level and to understand sources of variability observed in the behavioural results. The next sections present the corresponding analyses.

Individual analysis of MFT and accuracy: Congruent trials

We started by looking at whether the individual's strength of the price-preference bias would be correlated with MTF in congruent trials. Please remind that we hypothesised that subjects with a strong (i.e., significant) price-preference correlation would require more control precisely in congruent trials. This was the post-hoc explanation of the atypical reversal in the behavioural congruency effect in these participants, given that the strategic prior to choose the non-preferred item would have to be countermanded. In line

with this, we observed that in individuals whose accuracy is strongly associated with higher theta power in congruent trials, the more likely this person is to show the reversed congruency effect in behaviour (Figure 6B - left, Pearson, r = -.80, $p = 1.37 \times 10^{-7}$). Additionally, consistent with this explanation, individual MFT estimates in congruent trials were also positively correlated with individual correlation coefficients between preference and price (Figure 6C - left, r = -.51, p = .004). This reinforces the idea that for participants who usually prefer more expensive items, congruent trials required the need to regulate a conflict between a strategic prior (choose the non-preferred item) and the correct response.

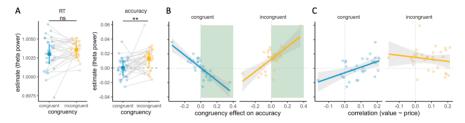


Figure 6. Mid-frontal theta predicts the value biases in choices. A. Estimates extracted from predicting response time (left) and accuracy (right) with (G)LMM using mid-frontal theta power, in congruent and incongruent conditions separately (plain coloured dots). Error bars represent 95% CI. Individual estimates are plotted behind and connected by grey lines. B-C. Correlations between individual theta power estimates (extracted from predicting accuracy) within congruent and incongruent trials and congruency effects on accuracy (probability to be correct in congruent minus incongruent trials) (B) and individual correlation coefficients between estimated prices and preferences (value) (C). Green areas represent expected values of congruency effects on accuracy.

Individual analysis of MFT and accuracy: Incongruent trials

Turning now to incongruent choices, please note that, MFT significantly predicted accuracy at the group level in incongruent trials, thus in principle suggesting that conflict detection and/or control facilitated correct responses. When unpacking this effect at the individual level, we observed that the stronger the behaviour was biased toward the preferred item overall, the better MFT power in that participant predicted accuracy (Figure 6B - right,

r = .68, $p = 3.80 \times 10^{-5}$). This is in line with our hypothesis that incongruent trials induce a stronger conflict, resulting in behavioural consequences and leading to the engagement of conflict-related brain mechanisms to overcome it. Furthermore, in contrast to congruent trials, no significant relation between theta estimates and the strengths of correlations between estimated price and preferences was found (Figure 6C - right, r = -.16, p = .21), suggesting that the prior toward responding with the non-preferred item (in a subgroup of participants) did not need to be controlled in these incongruent trials, and only the conflict elicited by the competition between price and value-based information was relevant.

Although, we only observed a small effect of congruency on the MFT power overall, we were able to demonstrate the strong relationship between theta oscillations and choice conflict at individual level (Pinner & Cavanagh, 2017).

Additionally, in multitasking situations, higher theta has been found to be associated with lower performance, suggesting that MFT power is a proxy to assess individuals' cognitive workload (Puma et al., 2018). In our study, we found higher MFT to be associated with better performance in incongruent trials (Spearman, r = .53, p = .003; without outliers: r = .60, p = .001) but not in congruent trials (Spearman, r = .28, p = .13; without outlier: r = .23, p = .22), suggesting that frontal theta reflects here the need for cognitive control and not the workload per se.

Individual analysis of MFT and accuracy: No-congruency trials

For completeness, similar analyses were conducted on trials without a congruency component, where both items are similarly valued. As previously reported, theta power did not emerge as a significant predictor of accuracy, and individual theta estimates exhibited no correlation with either the congruency effect on accuracy (r = -.17, p = .38) or the strength of the preference-forexpensive bias (r = .20, p = .30). These results further emphasize the specific influence of the preference-for-expensive bias on conflict monitoring and choice behaviour when a preferred alternative is present.

Finally, we investigated whether the distinct evolution of accuracy over time, contingent upon the presence of a preference-forexpensive bias (as illustrated in Figure S3), could be correlated with specific changes observed in MFT activity. We employed a LMM to predict MFT power as a function of time-on-task (run), congruency (C+ or C-), and the preference-for-expensive bias (significant or not) (Figure S7). We found a reduction of MFT activity (-450 to 50ms relative to the response) with the time spent on task $(\chi_1^2 = 12.94, p = 3.21 \times 10^{-4})$, mirroring prior reports in studies examining task-related MFT activity (Arnau et al., 2021; Beldzik et al., 2022). This effect could be attributed to learning and shortterm task automatization accompanied by a reduction in high-level cognitive control (Mohr et al., 2016). Interestingly, we also found a tendency for a three-way interaction between time-on task, congruency and the presence of the preference-for-expensive bias $(\chi_1^2 = 2.74, p = .098)$. Subsequent post-hoc analyses revealed a significant interaction between time-on-task and congruency for participants not exhibiting the preference-for-expensive bias $(\chi_1^2 = 7.35, p = .0067)$, wherein MFT decreased throughout the experiment in congruent choices, while it increased for incongruent choices. MFT activity has indeed been found to ramp up with mental fatigue (Tran et al., 2020), and this increase might be due to heightened cognitive exertion as participants strive to uphold task performance in the face of the price-value conflict. Conversely, no significant interaction emerged for participants with a preferencefor-expensive bias ($\chi_1^2 = .17, p = .68$), which could potentially explain the growing influence of their prior biases on their choices. prompting them to opt for the least preferred items more frequently than the preferred ones. Such adaptive behaviour might be favoured as cognitively less demanding.

The relation between price difference and theta reflects trial importance

The analyses of behavioural responses presented earlier pointed out that price difference modulates trial difficulty, with trials with large ΔP leading to faster and more accurate responses (hence, we can assume, easier). Importantly, the ΔP effect occurred across the board, regardless of congruency. An effect of price difference was also found on MFT power using LMM (<u>Table S6</u>, model m_2) and time-frequency analysis, which revealed a higher theta power for trials with a large ΔP (2 to 3 euros) compared to trials with a small ΔP (0 to 1 euro) from 280 until 20ms before response (Figure 7, t = 37.58, p = .007).

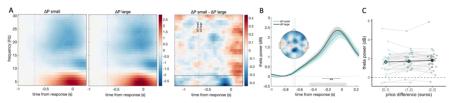


Figure 7. Easier but also more important trials are associated with higher mid-frontal theta power. A. Time-frequency analysis (responselocked) of trials with small differences in price (ΔP from 0 to 1 euro) between the two items (left) and trials with large price differences (ΔP from 2 to 3 euros) (middle) show an increase in theta power (dB) poststimulus presentation. Difference between small ΔP and large ΔP conditions (right) show a lower theta power before response. Vertical dashed lines represent mean RT. B. Average mid-frontal theta power (4-7Hz) of trials with small and large ΔP plotted over time. A significant cluster was found from 280 to 20ms before response ('**': p<.01) around which an analysis window was selected (grey shaded area: -450 to 50ms relative to response). The topographic head map represents the difference in theta power between trials with small and large ΔP over this analysis window. C. Average theta power predicted (Table S6- m_2) for ΔP conditions (coloured dot circled in black). Vertical black bars represent s.e.m. Grey lines connect individual subjects (observed data).

These results may seem counter intuitive, as theta power is generally found to increase with trial difficulty (e.g., with working memory load, Maurer et al., 2015) and correlate positively with RT (Cohen & Donner, 2013). However, in our case, price difference is not solely a proxy for trial difficulty, but it also correlates with trial importance for the subject's outcomes. Indeed, on erroneous trials, the difference in price between the two items penalizes (is added to) the participants' shopping cart. Consequently, while incorrect responses in trials with a small ΔP (a few cents) has little consequence on participants scores, errors in trials with large ΔP (a couple of euros or more) are greatly penalized. In previous literature, higher activity in the dACC has been associated with higher required effort but also with associated expectation of higher rewards or losses (Vassena et al., 2017; Cohen et al., 2009; Shenhav et al., 2013; Safavi & Dayan, 2022). In our case, these two features are conflated given that price difference correlates with both the difficulty (negatively) and trial importance (positively). We believe it is the greater losses associated with errors which could explain the larger theta activity observed with trials with large price differences.

In line with this hypothesis, we observed two main differences between the individual level of variations of MFT power with congruency conditions and with price difference. First, the congruency effect on accuracy (congruent more accurate than incongruent) tends to correlate with the congruency effect on MFT power (partial Pearson's correlation controlling for the preferencefor-expensive bias as it strongly correlates with the congruency effect on accuracy (r = -.44, p = .015; without outliers: r = -.41, p = .028): r = .39, p = .039; without outliers: r = .34, p = .077), while the variations of theta power with ΔP do not correlate with the effect of accuracy on ΔP (Spearman, r = -.039, p = .84; without outliers: r = .15, p = .45). These results suggest that performance accuracy as a function of price difference does not rely on theta power, as it can be the case in congruency conditions where conflict monitoring is necessary to ensure correct responses (Figure 6A).

Secondly, we observed that the more the MFT activity increases post-stimulus presentation in general, the less it increases with price difference (Pearson, r = -.40, p = .031; without outliers: Spearman, rho = -.52, p = .0055). This result may suggest individual differences in the cognitive workload of the task's objective difficulty (ΔP , short response deadline). Interestingly, this pattern is not observed across the congruency conditions

(Spearman, rho = -.042, p = .83; without outliers: Pearson, r = .073, p = .71) where MFT activity is overall found to be higher for incongruent compared to congruent trials regardless of individuals level of MFT power post-stimulus. It suggests that mid-frontal theta activity reflects mainly the conflict between price and value-based evidence and, when possible, it adapts to the magnitude of losses associated with potential errors in order to maximise performance.

Mid-frontal theta oscillations as a mechanism of cognitive control for the interaction between subjective value and estimated price

We previously found a general increase in MFT power in incongruent trials, where subjective value and objective information about price are in conflict, compared to congruent trials (Figure 5). To confirm the role of MFT as a common cognitive control mechanism, we sought to extend the results by looking at MFT activity following errors (Cavanagh et al., 2009; M. Cohen et al., 2009; Van Driel et al., 2012), and investigate how our experimental conditions may impact this effect. We analysed MFT activity in the 500ms window following responses, baselined with the 500ms window preceding stimulus onset, as a function of response accuracy (correct or incorrect), price difference, and congruency (Figure 8A). Using a LMM including these factors as fixed effects and subjects as random factor, we found a significant effect of response accuracy ($\chi_1^2 = 97.55$, $p < 2.2 \times 10^{-16}$) on post-response MFT with theta power being higher after errors. This replicates typical post-error Theta increase findings. We also found an interaction between ΔP and response accuracy $(\chi_1^2 = 44.78, p = 2.21 \times 10^{-11})$ with error-related theta (difference between MFT post-errors and post-correct responses) increasing with ΔP . In previous literature, increased MFT activity has been found for aware compared to unaware errors (Wang et al., 2020) and for errors associated with greater losses (Cohen et al., 2009). Here, incorrect responses in trials with larger ΔP are both more penalised (the price difference is added to participants' shopping cart) but probably also more detectable, which makes it difficult to disentangle these two sources.

A well-known post-error behaviour adjustment consists of slowing down the decision responses in the trial following an incorrect response (post-error slowing; Botvinick et al., 2001; Dutilh et al., 2012; Rabbitt, 1966). We addressed this adaptive mechanism and found significant post-error slowing for all ΔP magnitudes (small: $V = 405, p_{adj} = .004$, m e d i u m : $V = 455, p_{adj} = 2.75 \times 10^{-5}$, large: $V = 447, p_{adj} = 7.53 \times 10^{-4}$), demonstrating the validity and precision of participants' price estimations. What is more, we found an interaction of the post-error slowing with ΔP (LMEM, $\chi_1^2 = 7.58, p = .006$, Figure 8B) showing that response times are significantly slower following incorrect responses in trials with larger ΔP . Congruency did not interact with the amplitude of posterror slowing ($\chi_1^2 = .20, p = .90$).

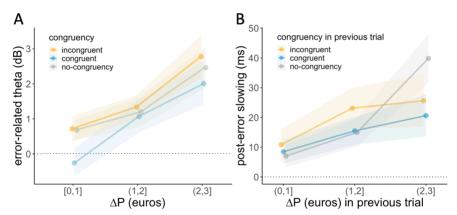


Figure 8. Errors in trials with large price difference are followed by larger MFT power post-response and longer response times in the subsequent trial. A. Differences between MFT power (in decibels) in the 500ms window (baselined with the 500ms window before response) after errors or after correct responses, depending on the price difference (ΔP) and the congruency (colours) in the current trials. B. Differences in RT between trials directly following errors or correct responses, depending on the previous trial's ΔP and congruency. Shaded areas represent s.e.m.

To test for the potential link between post-error slowing and posterror MFT increase, we used LMM to predict RTs based on the previous trial's MFT activity post-response and the response accuracy of the current trial. We found a significant interaction between these two factors ($\chi_1^2 = 13.12$, $p = 2.93 \times 10^{-4}$). Consistent with previous literature (see meta-analysis: Cavanagh & Shackman, 2015) and with our expectation, post-error MFT s i g n i f i c a n t l y p r e d i c t e d t h e n e x t t r i a l R T (t = 3.74, $p = 1.81 \times 10^{-4}$) but not MFT activity after correct responses (t = .044, p = .97), pointing out the role of MFT as a proxy for control after committing errors. However, post-error MFT amplitude did not predict accuracy in the subsequent trial (z = .73, p = .47). Additionally, MFT amplitude post-response was not affected by the current trial RT (t = .71, p = .48), as previously reported (Beldzik et al., 2022).

Finally, turning again to individual-level analysis, the amplitude of error-related MFT did not correlate with performance in general at individual level (*Pearson's*, r = .042, p = .82). However posterror slowing did (*Pearson's*, r = .41, p = .024), with participants who slowed down more after incorrect responses being also more accurate overall. Together, these results confirm the role of MFT in signalling the need for (and possibly exertion of) increased cognitive control in terms of trial-to-trial adaptation. In particular, they point out the relation of MFT to post-error slowing, a behaviour adaption reflecting the efficient use of control mechanisms to engage in a more cautious response mode.

Value biased conflict is not reflected in the motor-related activity

So far, we have interpreted the behavioural and EEG correlates for conflict as reflecting computations related to the decision process. However, one could assume that similar motor-related conflict regarding which response to effect, could have produced our results. In fact, decision-making processes and motor actions are not clear separable processes, since recent evidence points towards a parallel perspective of information processing where decision and action may coexist and interact. This notion is supported by evidence that choice action is frequently initiated before the completion of decision-making (Cisek & Kalaska, 2010; McKinstry et al., 2008;

Ozbagci et al., 2021; Resulaj et al., 2009). In this context, we do not aim to disentangle stimulus-related conflicts from motor-related conflicts. Instead, we focused on determining whether EEG correlates pertaining to motor preparation in the context of decision making reveal the presence of motor-related conflicts. To do so, we analysed neural corelates of motor activation through beta-band oscillations (13-30Hz, Figure S8) in parietal aeras and the lateralized readiness potential (LRP, Figure S9). Differences in the timing of motor activation between congruent and incongruent trials was not detected in beta but was detected in the LRP, with congruent trial latencies being shorter than incongruent trials. This latter result may reflect the difference observed in RT between congruency conditions.

The drift diffusion model fails to reproduce participants' choice behaviour

The drift diffusion model (DDM) is a powerful framework to model binary choices. In the value-biased decision-making literature, it has shown to reproduce human and animal behaviour by introducing different types of reward biased mechanisms. In order to provide better generalization of our findings, we intended to model participants' choice behaviour in our price minimisation task using a simple DDM comprising six free parameters (Table 1 and Figure 9). These parameters encompassed non-decision time, which was Gaussian-distributed with a specified mean (m_{nd}) and standard deviation (σ_{nd}). The simple model further included a drift rate (μ) governing the accumulation of evidence, and a lapse trial rate (p_L) introduced to account for odd trials, such as when responses were very fast and appeared unrelated to the presented stimuli. We also included an urgency signal, given the time pressure of the task. This urgency signal was modelled as a linear gain function characterized by an intercept σ_0 and a slope s_u .

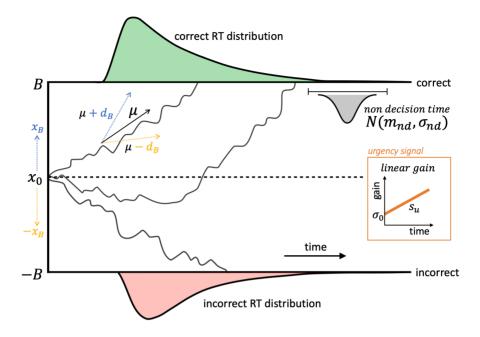


Figure 9. Illustration of the drift diffusion model (DDM). Evidence is accumulated in the decision variable (dx) over time until it reaches one of the decision thresholds (boundaries *B*). Three simulated trajectories of the decision variable are depicted, with a drift rate μ , and a starting point x_0 . RT comprises the decision time (duration for dx to reach a boundary) and the non-decision time (including encoding and response outputs), drawn from a normal distribution. Urgency is modelled as a linear gain which scales both noise and evidence accumulation. Value-biases, modelled as shifts in starting point x_B or drift rate d_B are depicted in their expected directions (blue: C+, yellow: C-). [back to Methods]

In addition, we modelled the value bias observed in both accuracy and RT by incorporating mechanisms impacting the evidence accumulation process through shifts in starting point or drift rate. We also introduced mechanisms which are independent of the information integration, such as errors in the mapping between the decision variable and the motor response (see <u>Methods</u> for more details). We observed that the model exhibiting the best fit (lowest BIC averaged across the participants, as shown in <u>Table S8</u>) was the one that encompassed a bias in the drift rate (d_B). The distribution of fitted d_B was found to be positive (Wilcoxon-test, W = 352, p = .013, Figure 10B), suggesting that the accumulation of evidence in favour of the preferred, compared to the nonpreferred item, occurs faster. This model additionally incorporated a non-zero probability for mapping errors to arise between the decision variable linked to the correct alternative and the motor output (p_{map}) . Introducing this mapping error possibility led to a modest reduction in the predicted accuracy, aligning it more closely with the observed accuracy.

However, overall none of the DDM models was able to predict the behavioural differences observed between the congruency conditions satisfactorily. The results show that the models overestimated the observed accuracy; in congruent trials, the slow errors, that may be related to the preference-for-expensive bias were not well predicted, while for incongruent trials, models failed to predict the fast errors caused by the selection of the preferred alternative (Figure 10A). Our attempts to introduce value biases which unfolded, or else faded out during the course of the trial, couldn't solve these issues (see Methods for more details).

To test whether the difficulty to reproduce the data was due solely to the value biases, we fitted separately trials with no congruency (small difference of estimated value between the two items). Here also, we encountered a similar deviation from the predicted accuracy, which was greater than the observed one (Figure S10A). Our attempts to increase the probability of errors using different mechanisms (leaky integration, decision-response mapping error) were not successful (Table S9) and the model giving the best predictions of the data was the simple DDM including six freeparameters (m_{nd} , σ_{nd} , p_L , s_u , σ_0 and $\mu - Figure S10B$).

As an additional control measure, we explored whether the difficulty of the DDM to model participants choice behaviour could be due to the presence of sequential effects. The details of our analysis are documented in the supplementary materials (Figure S11), and the results unveil a trend among participants to opt for the item displayed in a contrary position to the one previously chosen ('switch'), particularly in situations involving fast responses.

However, this phenomenon does not appear to affect accuracy significantly.

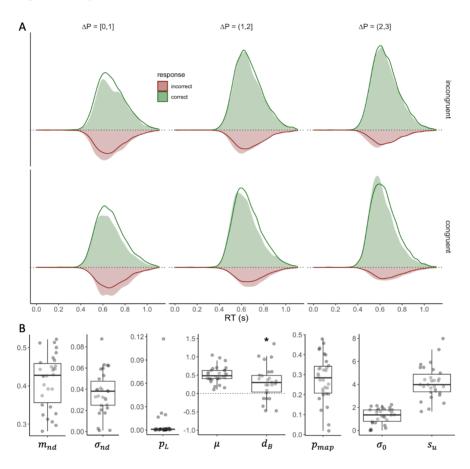


Figure 10. Participants' choice behaviour in the presence of congruency component cannot be fitted by a classical drift-diffusion model. A. Density distributions of observed (filled shapes) and predicted RTs (lines) extracted from the model with the highest goodness-of-fit, depending on the response accuracy (correct or incorrect), the congruency (incongruent or congruent) and the price difference between the two items (ΔP in euros). B. Distributions of the six fitted parameters, boxplots represent the 1st and 3rd quartiles of the data distribution, with thicker horizontal black lines corresponding to medians and whiskers extended to the largest value no further than 1.5 times the inter-quartile range (IQR). Behind is plotted individual data (N=30). The distribution of drift rate biases d_R was tested against zero ('*': p < .05).

Overall, the drift diffusion models we employed failed to predict the choice behaviour observed at our price minimisation task. We observe nonetheless that the fitted parameters remain coherent. The fitted non-decision times fall within a range reported in previous studies fitting perceptual and value-based decisions between pairs of complex realistic edible stimuli (Milosavljevic et al., 2010; Polanía et al., 2014). The distribution of fitted drift-rate biases was also significantly positive (Figure 10B) reflecting the advantage for preferred over non-preferred items and significantly correlated with the magnitude of participants' preference-for-expensive bias (Spearman, $\rho = -.46$, p = .011) but not with the difference in MFT power (-450 to 50 relative to response response) between incongruent and congruent trials (Spearman, $\rho = .28$, p = .13). These findings underscore the potential of the DDM to elucidate, albeit partially, the fundamental cognitive mechanisms underpinning the decision-making process at stake in this task. Specifically, while the preference-for-expensive bias appears to exert a relatively uniform impact across all choices, the cognitive conflict manifested through increased MFT may exhibit trialspecific variations, making it potentially more challenging to capture comprehensively within the framework of a classical DDM.

Discussion

To the best of our knowledge, this study stands as the first demonstration of intrinsic value biases (preferences) on objective decisions¹ in the absence of attentional anticipation or motor preparation based on pre-set response-reward contingencies. Our results using food stimuli and their intrinsic subjective preferences, replicate the outcomes found in those other tasks; the preferred alternative was selected faster and more often in case of rapid responses (Afacan-Seref et al., 2018; Corbett et al., 2023; Diederich, 2008; Diederich & Busemeyer, 2006; Mulder et al., 2012; Noorbaloochi et al., 2015; Summerfield & Koechlin, 2010). We found that the congruency effect between preference and

¹ Errors in price estimations are not affected by participants preferences.

choice-relevant information on RT was remarkably consistent across participants (Figure 3B) and over the duration of the task (Figure S2B), revealing that subjective value is able to bias online objective decisions, without the implication of prior expectations. Furthermore, the impact of the amount of goal-relevant evidence available on value biases has received limited attention in previous research and has yielded inconsistent findings. Some studies reported no discernible modulation of the biases driven by asymmetric payoffs (Noorbaloochi et al., 2015), while others noted an effect confined to accuracy (Corbett et al., 2023). In this study, we offer compelling evidence supporting the notion that value biases on decision behaviour remains unaltered by choice difficulty. This suggests that the impact of value on decision-making is rather automatic. Such proposition is supported by extant evidence which suggests the rapid and automatic encoding of value, even when it bears no relevance to the immediate task at hand (Lebreton et al., 2009; Moneta et al., 2023).

Moreover, while standard conflict tasks reveal that goal-irrelevant visual attributes exert a diminishing influencing on decisions as trials progress (Luo & Proctor, 2021; Ulrich et al., 2015), similar dynamics emerge in scenarios involving choices influenced by asymmetric reward with swift decisions, in particular, exhibiting a bias toward options linked to higher payoffs (Afacan-Seref et al., 2018; Corbett et al., 2023; Noorbaloochi et al., 2015; Summerfield & Koechlin, 2010). In this study, we successfully replicate these findings, further emphasizing the existence of a flexible mechanism redirecting resources away from preferred alternatives and toward task-relevant information. Our initial hypothesis postulated that cognitive control would assume this function, and our findings indeed support this premise. Specifically, incongruent trials characterized by value-price conflicts exhibited significantly greater MFT activity compared to congruent trials (Figure 5).

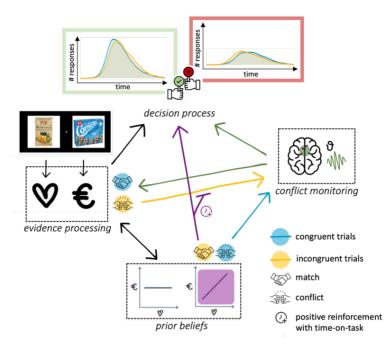


Figure 11. Proposed cognitive mechanisms occurring during our price minimisation task. Initially, value-based evidence is encoded, resulting in swift and accurate responses in congruent trials, as well as prompt errors in incongruent trials. Subsequently, information concerning the items' prices is encoded, triggering an increase in MFT activity in incongruent trials. This heightened MFT activity is in response to the conflicting evidence arising from the disparity between subjective value and prices. MFT plays a role in redirecting the decision process towards the evidence that aligns with the task goal, thereby upholding task performance. Furthermore, the processed evidence is subjected to comparison with preexisting prior beliefs. In scenarios where participants exhibit a significant preference-for-expensive bias (Figure 2), the accumulated information about the items may clash with their pre-existing bias, particularly in congruent trials. This potential conflict between the newly acquired evidence and prior beliefs might be resolved through MFT signalling. Alternatively, participants' prior belief may favour the non-preferred items by directly influencing the decision process or via the disengagement of the conflict signalling network in incongruent trials. Notably, this alternate pathway appears to gain prominence as participants progress through the experiment (Figures S5 and S6).

As expected, we also found that MFT served as an overall positive predictor of accuracy in incongruent trials and that the strength of this relationship correlated with the degree of individual value biases in decision-making (Figure 6A-B). This finding aligns with

prior research, underscoring the involvement of heightened cognitive control signalling to implement behavioural adjustment and enhance performance (Cooper et al., 2019; Kerns et al., 2004). What is more, while, at the group level, MFT activity was not associated to correct responses in congruent trials, suggesting no evident value-price conflict, it played a significant role for individuals exhibiting pronounced preferences for expensive items (Figure 6). Once again, the strength of this relationship correlated with participants' tendencies to exhibit behavioural bias toward their non-preferred alternative and suggests the existence of a conflict between, on one hand, the subjective value and price of the stimulus, and on the other hand, individuals' pre-existing beliefs concerning these attributes. We posit that this conflict elucidates why participants with significant preference for expensive items did not manifest the anticipated accuracy effects in faster trials and even displayed opposite congruency effects in slower trials (Figure 4). In these cases, their priors guided decisions away from the preferred item, which they usually associate as more expensive (and hence, incorrect, response).

As initially proposed in the original versions of the conflict monitoring theory (Botvinick et al., 2001), previous results has shown that conflict monitoring, as gauged by ACC activity and MFT power increases, is not restricted to motor conflicts (Kerns et al., 2004) and extends to perceptual (Drew et al., 2022; Jiang et al., 2018; Nigbur et al., 2012) and stimulus-stimulus conflicts (Drew & Soto-Faraco, 2023; Marly et al., 2023; Morís Fernández et al., 2018). Our findings contribute to further broaden the theory by demonstrating high level stimulus conflict between two different properties of the same stimulus (Ruzzoli et al., 2020), as well as conflict between stimulus properties and pre-existing beliefs (priors). Moreover, our results reinforce earlier discoveries indicating that subjective value evidence skews decision-related signals in higher cortical regions (Rorie et al., 2010; Summerfield & Koechlin, 2010). These findings serve as a foundational basis for advancing our comprehension of the neural mechanisms underlying the flexible behavioural adaptations in response to conflict.

Concerning the prior expectations associated with stimuli, they have been consistently demonstrated to impact both perception (Bar, 2004; Summerfield & Koechlin, 2008) and decision-making (Kelly et al., 2020; Hanks et al., 2011; Ratcliff, 1985; Mulder et al., 2012) through reciprocal interactions between top-down priors and bottom-up inputs. In the latter cases, adjustments in either the starting point (Bogacz et al., 2006; Cho et al., 2002; Mulder et al., 2012; Wagenmakers et al., 2008) or the drift rate of the evidence accumulation process (Hanks et al., 2011; Ratcliff, 1985) have been reported, indicating a preference for the alternative that is more often correct. However, these studies involve alternatives with unequal prior probabilities of being correct for which the associated motor outputs are known. In contrast, in the present study, priors could not drive anticipatory attentional or motor effects, as they require first identifying and categorising the items in order to then map them onto prior representations of how properties such as subjective values and price are represented. This likely explains why in our case, a significant bias in the drift rate predominantly accounts for the data and aligns with individuals' preference-forexpensive bias. Additionally, this may clarify why the prior's impact increases over time within a trial, contrary to the typical finding where the effect of the prior diminishes as more evidence is accumulated (Gold et al., 2008).

Moreover, both behavioural and neural findings in the present study consistently demonstrated that the impact of prior stimuli expectations was dynamic and increased over time within the task. Basing decisions on prior representations might indeed constitute an adaptive strategy that is less cognitively demanding than invoking stronger cognitive control mechanisms, manifested by increases in MFT activity. Specifically, anticipatory effects with prior belief of outcome distributions indicate that responses linked with the less probable stimulus tend to be slower and less frequent (Mulder et al., 2012; Wagenmakers et al., 2008). However, in the case of participants exhibiting a significant preference-for-expensive bias, the expected likelihood of the preferred option being correct is diminished, leading them to select the preferred option less often, but also more rapidly. These findings suggest, in our experimental protocol, the coexistence of a competitive interplay between mechanisms guided by prior beliefs and those influenced by subjective value, where the influence of value prevails primarily in relation to reaction time and appears decoupled from choice accuracy. Indeed, even though value biases choice behaviour in a seemingly automatic manner (independently on the extent of goalrelevant evidence available), its effect on response accuracy can be countermanded while its impact on RT persists. Further investigations are needed to gain a deeper comprehension of the underlying cognitive and neural processes and these intricate interactions.

Additionally, even though statistically significant in only half of the participants examined, we cannot disregard the possibility that the preference-for-expensive bias is inherently widespread within our sample group and could potentially manifest given a larger selection of edible items. Indeed, price and perceived quality have been shown to be positively correlated (Rao & Monroe, 1989), possibly forming the basis for a corresponding positive relationship between subjective values and prices. We posit that the overall reduction in accuracy observed as the trial progresses, particularly in congruent trials—an aspect that may seem perplexing—could potentially be attributed to this bias.

This study underscores the generality and intricacy of mid-frontal theta (MFT) oscillations as a cognitive control mechanism. In addition to conflict-related MFT, our findings shed light on its involvement in post-error adjustments, consistent with prior research (Cavanagh et al., 2009; M. Cohen et al., 2009; Van Driel et al., 2012). Notably, we observed that the increase in error-related MFT is heightened with greater price differences (ΔP) (Figure 8A). This modulation may stem from the heightened salience of errors in trials with larger ΔP , as supported by prior work demonstrating that post-error MFT is influenced by error awareness (Wang et al., 2020). Alternatively, the penalty aspect of large ΔP , as it deducts

from participants' performance in case of incorrect responses, makes it possible the concomitant role of the trials' importance or expected costs on these fluctuations (Cohen et al., 2009). However, it is worth noting that recent evidence fails to support such effect (Frömer et al., 2021).

Regarding MFT activity during the decision process, our paradigm implied an inverse relationship between trial difficulty, indexed by less accurate and slower responses as ΔP decreases (Figure S2), and trial importance or potential cost, which increases with ΔP . This finding appears contrary to our initial expectation, which was based on prior literature demonstrating that ACC and MFT activity increases with task difficulty (Shenhav et al., 2014; Pochon et al., 2008; Botvinick, 2007). However, the ACC is sensitive to various signals, including choice value and effort cost (Croxson et al., 2009; Klein-Flügge et al., 2016), which may confound its direct relationship with task difficulty (Botvinick et al., 2001; Kolling et al., 2016), as also challenged by recent studies (Umemoto et al., 2023; Castro-Meneses et al., 2020). Instead, we interpret the increase in MFT activity with ΔP as an effect of trial importance, where greater cognitive control is needed when larger losses are at stake. This interpretation aligns with the expected value of control theory (Shenhav et al., 2013, 2016), which posits the role of the dACC in weighing the costs and benefits associated with decisions to optimize cognitive resource allocation. Indeed, individuals are shown to engage more cognitive control areas when they expect higher rewards or losses (Alexander & Brown, 2011; Brown & Braver, 2007; Rushworth & Behrens, 2008).

Interestingly, we found that the relationship between MFT activity and ΔP depends on basal Theta activity during the decision process. This suggests that, at an individual level, Theta is modulated in response to task importance only when it is not already high owing to task demands. MFT related to cognitive load has indeed been shown to exhibit large individual variability (Gevins & Smith, 2000; Klimesch et al., 1999). Additionally, when comparing congruent and incongruent trials, we observed that the increase in MFT during the latter, compared to the former, is not contingent on the basal activation of task-related MFT. In short, the presence of a ceiling effect affecting MFT activity related to expected loss, but not conflict-related MFT, suggests the existence of multiple levels of cognitive control signaling. Notably, the value-price conflict appears to have a more automatic effect, seemingly independent of perceived task demands.

Lastly, prior studies have reported both decreases (Arnau 2021; Beldzik 2022) and increases (Tran et al., 2020; Wascher et al., 2014) in task-related MFT with time-on-task. Our findings reconcile these divergent findings by revealing complex modulations of task-related MFT with time spent on the experiment. These modulations differ depending on the presence of both a value-price conflict and a prior belief binding subjective values and prices at an individual level (Figure S7). It seems improbable that increased fatigue or disengagement in the task may have caused these complex interactions. Instead, these results indicate that Theta is flexibly modulated over the course of the experiment to more efficiently allocate cognitive resources.

Further investigations are warranted to gain a deeper understanding of the multifaceted and dynamic nature of MFT signaling, its underlying neural networks (Zuure et al., 2020; Töllner et al., 2017), and its potentially distinct roles, such as conflict processing or error correction (Muralidharan et al., 2023; Töllner et al., 2017; Beldzik et al., 2022).

In this study, we opted to delve into the cognitive mechanisms underlying value-biased decisions within a realistic experimental context. While we deem this approach crucial for comprehending human behaviour in genuine settings, it also introduces intricacies that can pose challenges. Primarily, the experimental conditions are built on the items' values and prices, which are both estimated. In regard to values, we managed this uncertainty by constructing our congruency conditions around substantial preference disparities. Concerning prices, our observations of slower response patterns and increased MFT activity following errors, even for minor price differences (less than one euro), suggest participants' estimations were remarkably precise and consistent. However, estimations errors leading to mis-categorisations of the trials cannot be entirely excluded and may have added noise in our results.

Among the various objective attributes of edible items, our decision to inquire about prices stemmed from the frequent real-world practice of estimating prices (potentially more common than explicitly assessing weight or size dimensions). Furthermore, such estimation necessitates an initial encoding of the product's identity. This differs from prior experimental designs where participants selected between edible items based on the extent of background they covered on the screen, yielding no discernible effect of subjective value (Polanía et al., 2014).

Employing real-life edible items also introduces an inherent challenge linked to the potential variability in participants' familiarity with the presented products. This variability could impact the precision or confidence of their initial estimations of value and price. Furthermore, this familiarity factor might have exerted an influence during the subsequent choice phase. Specifically, items that participants were more familiar with could have been more quickly encoded, and facilitated a faster retrieval of their associated features or garnered a more substantial share of attention during the decision-making process. We tried to minimise the possible impact of this by first explicitly asking participants about the edible items they did not recognise and removed them from the subsequent task phases. Additionally, we collected a high number of trials for each participant (more than a thousand on average, see Table S1) to reduce the potential impact of the familiarity confound.

The potential complexity associated with the cognitive mechanisms involved in the task employed, and the variability inherent in the processing of each stimulus could directly contribute to the challenges encountered in accurately predicting the data using the drift diffusion model framework. We therefore contemplated the possibility that some fundamental tenets of the drift-diffusion framework might not have been optimally suited to the task at hand. First, we questioned whether the assumption that the decision variable relies on sequential sampling might have encountered limitations within this specific experimental context due to the accumulation of both external and internal evidence. Indeed, existing literature suggests that patients with hippocampal damage display impairments in value-based decisions, implying a role of memory in such processes (Foerde et al., 2013; Palombo et al., 2015). However, studies have also shown that choice behaviour in value-based tasks conforms to the sequential sampling model's regularities (Krajbich et al., 2010; Milosavljevic et al., 2010; Polanía et al., 2014), even when memory retrieval is clearly required (Gluth et al., 2013), indicating that memory retrieval and sensory evidence accumulation might, to some extent, share neural networks (Shadlen & Shohamy, 2016). Here the complex interaction between value, task-relevant evidence and participants prior's belief may be more difficult to formally dissociate in time. Second, in our attempt to account for within-participant variation in the processing of stimuli, we introduced factors like gaussian distributed non-decision time to accommodate trial-specific differences. However, a more substantial concern pertains to the assumption of the drift diffusion model (DDM) that the drift rate and decision threshold remain constant across trials. Our findings indeed reveal that the decision process is susceptible to transient biases (stemming from value and prior beliefs), which can be counteracted through dynamic enhancements in cognitive control, revealing that adjustments occur within the course of a decisionmaking process. In the case of decisions influenced by priors, the implementation of a neurologically informed model utilising EEG correlates of evidence accumulation and motor preparation enabled the incorporation of drift and urgency rate adjustments, resulting in improved predictive accuracy of choice behaviour (Kelly et al., 2020). Recent studies employing tasks involving conflict processing have used the hierarchical drift-diffusion model (HDDM; Wiecki et al., 2013) to introduce trial-specific variations in mid-frontal theta (MFT) activity. These studies have demonstrated its impact on various parameters influencing the choice process, such as the starting point, drift rate, and decision threshold (Guan et al., 2023; Castagna et al., 2023; Frank et al., 2015). These results are indeed promising, but they also highlight the challenges in identifying the specific roles of conflict-related MFT in shaping decision processes. Moreover, our results demonstrate that fluctuations of MFT activity throughout the experiment (Figure S7) is not associated with similar variations in choice behaviour (Figures S3 and S4) revealing that the effect of MFT on the decision process may be indirect or in interaction with other brain structures. Additional research is warranted, particularly employing intracortical recordings, to more precisely identify the sources of the rapid and dynamic MFT activity observed, as well as the specific neural networks it is intricately involved with.

In conclusion, this study effectively underscores the impact of inherent preferences on objective decision-making, in the absence of anticipatory preparation. This finding further strengthens the notion that value is swiftly and automatically encoded, preceding and irrespective of the quantity of goal-relevant information available. Additionally, it introduces a novel cognitive model wherein MFT oscillations contribute to steering the decision process towards goal-relevant evidence, thus overcoming online value biases. Finally, the use of a more ecological experimental setting, with realistic stimuli, has unveiled the implications of complex processes intertwined with participants' prior representations.

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Supplementary figures

congruency		% of trials				number of trials				
		by ΔP		total	by ΔP			total		
	small	mediu	large		small	mediu	large	-		
no-	9.6±2.	9.6±3.9	6.2±2.1	25.5±	120±38	118±37	78±29	316±4		
congruent	9.7±3. 0	10.4±2. 8	10.2±3.	30.3±	122±40	131±40	128±41	381±9		
incongruent	9.5±3.	11.0±2. 7	10.6±2. 6	31.1±	119±41	138±38	134±38	391±9		
total	28.9±	31.0±	$\underset{7.4}{27.0\pm}$	86.9± 10.9	361±1	$\underset{82}{387\pm}$	340±	1088± 199		

Table S1. Average percentage and total number of trials per subject (\pm SD) included in the analyses for all congruency and price difference (Δ P) conditions. [back to Methods] [back to Discussion]

Sampling Units		N total of N Subject	pservations = 35017 ts = 31								
Model specification	Model	Nested	Fixed Effects	Random Effects		Model	fit		LF	RT Test aş	gainst nested
Hoder specification	name	model	added	Subjects	AIC	BIC	LL	df	df	χ²	р
Random effect only	m_{Null}	-	-	intercepts	40634.7	40651.7	-20315.7	2	-	-	-
congruency	m_1	m_{Null}	congruency	intercepts	40594.9	40628.8	-20293.5	4	2	43.81	3.06×10 ⁻¹⁰ ***
$congruency + \Delta P$	m_2	m_1	ΔΡ	intercepts	39115.7	38158.1	-19552.9	5	1	1481.2	<2.2×10 ⁻¹⁶ ***
$congruency + \Delta P + RT$	m_3	m_2	RT	intercepts	39005.3	39056.1	-19496.6	6	1	112.48	<2.2×10 ⁻¹⁶ ***
$\begin{array}{c} congruency + \Delta P + RT + \\ congruency : \Delta P \end{array}$	m_4	m_3	congruency : ΔP	intercepts	39007.9	39075.6	-19495.9	8	2	1.42	.49
$\begin{array}{c} congruency + \Delta P + RT + \\ congruency : RT \end{array}$	m_5	m_3	congruency : RT	intercepts	38793.4	38861.1	-19388.7	8	2	215.91	<2.2×10 ⁻¹⁶ ***
$\begin{array}{c} congruency + \Delta P + RT + \\ congruency : RT + \\ \Delta P : RT \end{array}$	m_6	m_5	$RT:\Delta P$	intercepts	38792.9	38869.1	-19387.5	9	1	2.46	.12
$\begin{array}{l} congruency + \Delta P + RT + \\ congruency : RT + \\ congruency : \Delta P : RT \end{array}$	m_7	m_5	$\mathbf{RT}: \Delta \mathbf{P}$	intercepts	38796.1	38889.2	-19387.1	11	3	3.24	.36

Table S2. Selection of GLMM predicting accuracy. Each model is fitted to the data and compared to a simpler nested model using Likelihood Ratio Tests (LRT). For each model is reported its Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), log-likelihood (LL) and degrees of freedom (df). [back to Methods] [back to Results]

Fixed effects	estimate	SE	95% CI	Z	p
Intercept (no congruency)	.72	.14	[.45 .99]	5.20	1.99×10 ⁻⁷ ***
Congruency - congruent vs. no-congruency	.13	.03	[.05 .2]	3.99	2.00×10 ⁻⁴ ***
Congruency - incongruent vs. no-congruency	.01	.03	[07 .08]	0.23	.97
Congruency - congruent vs. incongruent	.12	.03	[.05 .19]	3.99	2.00×10 ⁻⁴ ***
ΔP (no congruency)	.56	.02	[.53 .59]	36.26	1.27×10 ⁻¹⁵⁵ ***
RT (no congruency)	84	.17	[-1.1850]	-4.86	.012 *
Congruency: RT-congruent vs. no-congruency	-1.99	.23	[-2.45 -1.53]	-8.47	8.02×10 ⁻⁹ ***
$Congruency: RT-incongruent vs. \ no-congruency$	1.31	.23	[.86 1.77]	5.66	9.62×10 ⁻⁴ ***
$Congruency: RT-congruent \ vs. \ incongruent$	-3.30	.23	[-3.75 -2.86]	-14.5	1.16×10 ⁻⁴⁷ ***
Random Effects	variance	SD	ICC		
Subject (intercept)	.372	.610	.04		
Model Fit	marginal	conditional			
<i>R</i> ²	.082	.119			

Table S3. Report of the model predicting accuracy the best (model m_5 –

Table.S2). For each significant effect is reported the estimate, standard error (SE), 95% confidence interval (CI), z statistics and *p*-value. [back to Results]

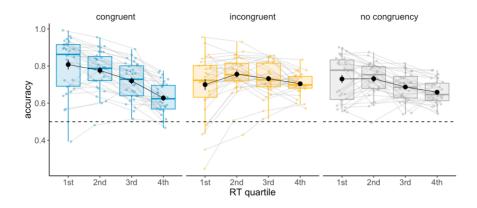


Figure S1. The probability to be correct as a function of response time (RT) decreases predominantly in congruent trials. Accuracy depending on the RT quartile (1st: faster, 4th: slower) and the congruency condition (colours). Black dots represent the mean and vertical bars the s.e.m. Individual observed data is plotted (colour dots) for each congruency condition and linked with grey lines. Boxplots represent the 1st and 3rd quartiles of the data distribution, with thicker horizontal black lines corresponding to medians and whiskers extended to the largest value no further than 1.5 times the inter-quartile range (IQR). Behind is plotted individual data and connected by grey lines (N=31). [back to Results]

Sampling Units		N total ob N Subject	servations = 35017 s = 31										
Model specification	Model	Nested	Fixed Effects	Random Effects		Model fit				LRT Test against nested			
1	name	model	added	Subjects	AIC	BIC	LL	df	df	χ²	р		
Random effect only	m_{Null}		-	intercepts	-18735	-18709	9370.4	3	-	-	-		
accuracy	m_1	m_{Null}	accuracy	intercepts	-18915	-18881	9461.6	4	1	182.34	<2.2×10 ⁻¹ ***		
accuracy + congruency	m_2	m_1	congruency	intercepts	-18977	-18926	9494.6	6	2	66.088	4.69×10 ⁻¹ ***		
accuracy + congruency + ΔP	m_3	m_2	ΔP	intercepts	-19251	-19192	9632.6	7	1	275.89	<2.2×10 ⁻¹ ***		
$accuracy + congruency + \Delta P$ + accuracy : congruency	m_4	m_3	accuracy : congruency	intercepts	-19403	-19326	9710.3	9	2	155.47	<2.2×10 ⁻¹ ***		
accuracy + congruency + ΔP + accuracy : congruency + congruency : ΔP	m_5	m_4	congruency : ΔP	intercepts	-19400	-19307	9710.8	11	2	1.09	.58		
$accuracy + congruency + \Delta P$ + accuracy : congruency + accuracy : ΔP	m_6	m_5	accuracy : ΔP	intercepts	-19409	-19324	9714.6	10	1	8.52	.003 **		
accuracy + congruency + ΔP + accuracy : congruency + accuracy : congruency : ΔP	m_7	m_6	accuracy : congruency : ΔP	intercepts	-19402	-19284	9715.2	14	4	1.37	.85		

Table S4. Selection of LMM predicting reaction times (log-transformed). Each model is fitted to the data and compared to a simpler nested model using Likelihood Ratio Tests (LRT). For each model is reported its Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), log-likelihood (LL) and degrees of freedom (df). [back to Results]

Fixed effects	estimate	SE	95% CI	t	p
Intercept (no congruency)	39	.01	[4136]	-31.58	1.04×10 ⁻²⁸ ***
Accuracy - incorrect vs. correct	007	.005	[017 .003]	-1.46	.14
Congruency - congruent vs. no-congruency	006	.003	[012 .001]	-2.04	.10
Congruency-incongruent vs. no-congruency	005	.003	[012 .001]	3.92	.12
Congruency-congruent vs. incongruent	-3.32×10 ⁻³	.003	[006006]	12	.99
ΔP (no congruency)	014	.002	[019010]	-6.39	1.64×10 ⁻¹⁰ ***
Accuracy (correct) : Congruency					
congruent vs. no-congruency	026	.003	[033019]	-8.82	<.0001 ***
incongruent vs. no-congruency	.007	.003	[.000 .014]	2.51	.032 *
congruent vs. incongruency	-033	.003	[039027]	-12.26	<.0001 ***
Accuracy (incorrect) : Congruency					
congruent vs. no-congruency	.015	.005	[.004 .025]	3.10	.0056 **
incongruent vs. no-congruency	018	.005	[029007]	-3.92	.0003 ***
congruent vs. incongruency	.032	.005	[.022 .043]	7.20	<.0001 ***
Accuracy : ΔP	008	.003	[013003]	-2.91	.004 **
Random Effects	variance	SD	ICC		
Subject (intercept)	.03	.17	.11		
Model Fit	marginal	conditional			
<i>R</i> ²	.018	.126			

Table S5. Report of the model predicting RT the best (model m_6 – Table.S4). For each significant effect is reported the estimate, standard error (SE), 95% confidence interval (CI), t statistics and p-value. [back to Results]

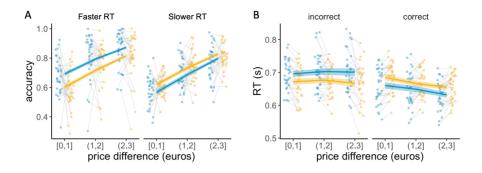


Figure S2. Congruency effects on choice behaviour are not modulated by the amount of goal-relevant evidence present. Lines represent the predicted mean accuracy (A) and RT (B) using mixed effect models, depending on the price difference between the two alternatives (ΔP), the congruency and the response time (RT - median split) (A) or the response accuracy (B). Shaded areas represent the predicted standard error of the mean (s.e.m.). Observed averages (colour dots) and their associated s.e.m. (vertical bars) are plotted behind. [back to Results] [back to Discussion]

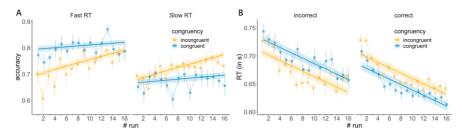


Figure S3. Participants' choices are more accurate with time-on-task, especially for incongruent trials, while they get faster, equally for incongruent and congruent trials, throughout the experiment. Lines represent the predicted mean accuracy (A) and RT (B) using mixed effect models, depending on the run presentation order, the congruency and the response time (RT - median split) (A) or the response accuracy (B). Shaded areas represent predicted standard errors of the mean (s.e.m.). Observed averages (colour dots) and their associated s.e.m. (vertical bars) are plotted behind. [back to Results] [back to Discussion]

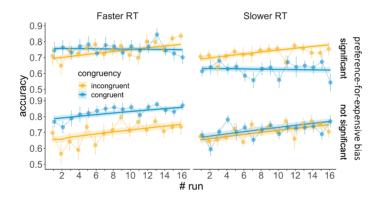


Figure S4. Participants' choices accuracy changes differently throughout the experiment depending on the presence of the preference-for-expensive bias. Lines represent the predicted mean accuracy using a GLMM, depending on the run presentation order, the response time (RT - median split), the congruency and the presence of a significant preference-for-expensive bias. Shaded areas represent the predicted standard error of the mean (s.e.m.). Observed averages (colour dots) and their associated s.e.m. (vertical bars) are plotted behind. [back to Results] [back to Discussion]

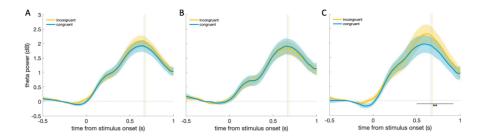


Figure S5. Stimulus-locked MFT. Averaged mid-frontal theta power (4-7Hz) of congruent and incongruent correct trials plotted over time for all participants (A) or for the subset of participants with (B) or without (C) a significant preference-for-expensive bias. A significant cluster was found only for participants not exerting the preference-for-expensive bias, from 500 to 920ms after stimulus onset (t = 60.09, $p_{adi} = .0088$).

[back to Methods] [back to Results]

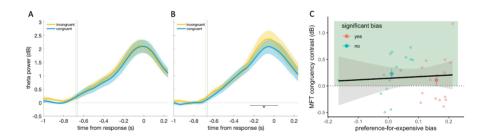


Figure S6. The magnitude of the preference-for-expensive bias does not explain individual difference in the congruency effect on MFT. A-B. Averaged mid-frontal theta power (4-7Hz) of congruent and incongruent correct trials plotted over time-in-trial (response locked) for the subset of participants with (A) or without (B) a significant preferencefor-expensive bias. A significant cluster was found only for participants not exerting the preference-for-expensive bias, from -240 to 40ms relative to the response (t = 32.03, $p_{adj} = .028$). C. Difference in MFT activity between incongruent and congruent trials depending on the magnitude of the preference-for-expensive bias and its significance (for p<.05, colours). Darker colour dots with vertical bars represent the means and s.e.m. for the group with (red) or without a significant bias (blue). The green area represents the expected MFT congruency contrast. [back to Results] [back to Discussion]

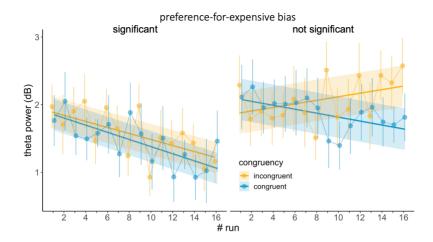


Figure S7. Participants' MFT activity changes differently throughout the experiment depending on the presence of the preference-forexpensive bias. Lines represent the predicted mean MFT power (in dB) using a LMM, depending on the run presentation order, the congruency and the presence of a significant preference-for-expensive bias. Shaded areas represent the predicted standard error of the mean (s.e.m.). Observed averages (colour dots) and their associated s.e.m. (vertical bars) are plotted behind. [back to Results] [back to Discussion]

Sampling Units		N total obs N Subjects	ervations = 22488 = 30								
Model specification	Model	Nested	Fixed Effects added	Random Effects	Model fit				LRT Test against nested		
	name	model	Three Entres added	Subjects	AIC	BIC	LL	df	df	χ^2	p
Random effect only	m_{Null}	-	-	intercepts	128138	128162	-64066	3	-	-	-
congruency	m_1	m_{Null}	congruency	intercepts	128135	128175	-64063	5	2	6.43	.040 *
$congruency + \Delta P$	m_2	m_1	ΔP	intercepts	128131	128179	-64060	6	1	6.29	.012 *
$\begin{array}{c} congruency + \Delta P + \\ congruency : \Delta P \end{array}$	m_3	m_2	congruency : ΔP	intercepts	128134	128198	-64059	8	2	1.20	.55

Table S6. Selection of LMM predicting mid-frontal theta power (-450 to 50ms relative to response). Each model is fitted to the data and compared to a simpler nested model using Likelihood Ratio Tests (LRT). For each model is reported its Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), log-likelihood (LL) and degrees of freedom (df). [back to Results]

Fixed effects	estimate	SE	95% CI	t	p
Intercept (no congruency)	1.59	.21	[1.18 2]	7.61	5.25×10 ⁻⁹ ***
Congruency - congruent vs. no-congruency	08	.007	[22 .06]	-1.11	.27
Congruency – incongruent vs. no-congruency	.08	.007	[05 .22]	1.19	.23
Congruency - congruent vs. incongruent	16	.007	[2903]	-2.49	.013 *
ΔΡ	.08	.003	[.02 .15]	2.51	.012 *
Random Effects	variance	SD	ICC		
Subject (intercept)	17.36	4.17	.06		
Model Fit	marginal	conditional			
R ²	.001	.063			

Table S7. Report of the model predicting mid-frontal theta power the best (model m_3 – Table.S6). For each significant effect is reported the estimate, standard error (SE), 95% confidence interval (CI), t statistics and p-value. [back to Results]

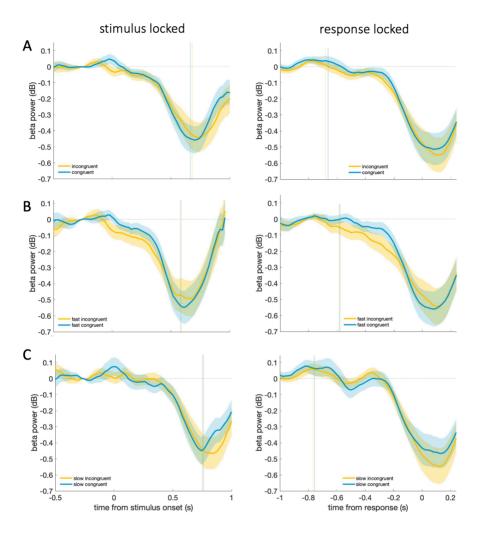


Figure S8. Beta desynchronization associated with motor response preparation doesn't differ in congruent and incongruent trials. Beta power (13-20Hz) contrasted between contra- and ipsilateral motor areas relative to motor response as a function of time, and locked either to the stimulus onset (left) or to the response (right). All incongruent (yellow) and congruent (blue) correct trials are displayed in **A**, while only the faster and slower trials (median split on the RT) are displayed in **B** and **C** respectively. Shaded areas represent the s.e.m. and vertical bars represent the mean RT (left) or time of stimulus onset (right). We observed the typical beta desynchronization contralateral to the side of motor response before the movement onset. However, we did not observe any differences in incongruent compared to congruent trials (**A**). Especially, in the slower trials we did not observe an initial activation of opposite response motor pathway (**C**). [back to Results]

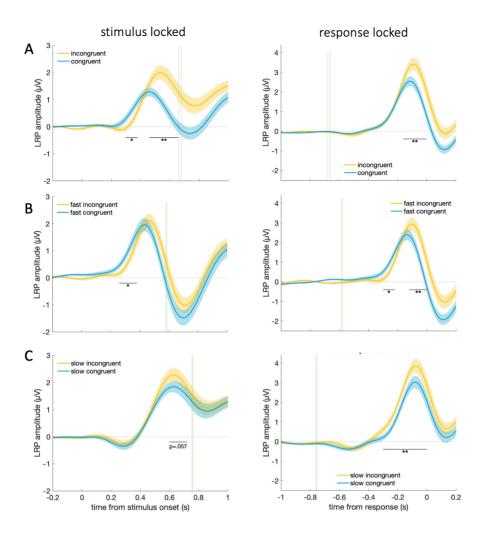


Figure S9. Motor response preparation, measure through LRP, is initiated earlier in congruent, compared to incongruent trials. Lateralized readiness potentials (LRP) as a function of time, and locked either to the stimulus onset (left) or to the response (right). All incongruent (yellow) and congruent (blue) correct trials are displayed in **A**, while only the faster and slower trials (median split on the RT) are displayed in **B** and **C** respectively. Shaded areas represent the s.e.m. and vertical bars represent the mean RT (left) or time of stimulus onset (right). Significant differences or trends between congruent and incongruent trials are indicated by the horizontal black lines ('*': $p_{adj} < .05$, '**': $p_{adj} < .01$). We

observed difference in the peak, with higher amplitude for incongruent compared to congruent trials, and in the timing of motor response activation, with congruent trial preceding incongruent trials especially in fast trials (**B**). In slow trials, we observed an initial negative bolus, corresponding to the activation of the motor pathway opposite to the final response, but it didn't significantly differ between the congruency conditions (**C**). [back to Results]

ias d_B	as x_B	Mapping errors P_{map}		tegration t_D			
Drift rate bias d_B	Starting bias x_B	Mapping e	Leak e	Delayed integration	Decision variable (dx)	Averaged nLL	Averaged BIC
					$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-251.54	-442.30
×					$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW + d_B \bullet C$	-256.99	-443.07
×					$((\mu \bullet \Delta P + d_B \bullet C) \bullet u(t) \bullet dt) + u(t) \bullet dW$	-256.64	-442.37
	×				$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-256.99	-443.07
		×			$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-257.83	-444.76
			×		$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW - \ell$	-253.46	-436.01
×		×			$(\boldsymbol{\mu} \boldsymbol{\cdot} \Delta \boldsymbol{P} \boldsymbol{\cdot} \boldsymbol{u}(t) \boldsymbol{\cdot} \mathrm{d}t) + \boldsymbol{u}(t) \boldsymbol{\cdot} \mathrm{d}W + d_B \boldsymbol{\cdot} \boldsymbol{C}$	-264.38	-447.71
×		×			$((\mu \bullet \Delta P + d_B \bullet C) \bullet u(t) \bullet dt) + u(t) \bullet dW$	-263.51	-445.98
	×	×			$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-263.79	-446.54
×			×		$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW + d_B \bullet C - \ell$	-258.95	-436.85
×					$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW + (d_B \bullet C)/(t+1)$	-256.94	-442.97
×					$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW - d_B \bullet C \bullet t$	-251.53	-432.15
×					$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW + \frac{d_{B_1} \bullet C}{t+1} - d_{B_2} \bullet C \bullet t$	-256.86	-432.68
×		×			$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW + \frac{d_{B_1} \bullet C}{t+1} - d_{B_2} \bullet C \bullet t$	-262.59	-434.01
×	×	×			$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW - d_B \bullet C \bullet t$	-263.90	-436.62
×	×	×			$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW - d_B \bullet C_+ \bullet t$	-263.92	-436.66
×					$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW + (d_B \bullet C - t)$	-256.90	-432.77
×		x			$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW + (d_B \bullet C - t)$	-255.72	-440.52
				×	$I_{t>t_D}(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-252.77	-434.63
				×	$I_{t \le t_D}(\mu_1) + I_{t > t_D}(\mu_2 \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-258.20	-425.23
×				×	$I_{t \le t_D}(d_B \bullet C) + I_{t > t_D}(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-257.61	-434.19

Table S8. Summary of the DDMs used to model participants' choice behaviour in the presence of congruency component. Goodness-of-fits are reported through negative log-likelihoods (nLL) and Bayesian information criteria (BIC). [back to Results]

Mapping errors $ p_{map}$	¢	Delayed integration t_D			
Mapp	Leak	Delay	Decision variable (d <i>x</i>)	Averaged nLL	Averaged BIC
			$(\boldsymbol{\mu} \boldsymbol{\cdot} \Delta \boldsymbol{P} \boldsymbol{\cdot} \boldsymbol{u}(t) \boldsymbol{\cdot} \mathbf{d} t) + \boldsymbol{u}(t) \boldsymbol{\cdot} \mathbf{d} W$	-86.54	-117.85
×			$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-88.72	-113.01
	×		$(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW - \ell$	-87.34	-110.27
		×	$I_{t>t_D}(\mu \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-86.66	-108.89
		×	$I_{t \leq t_D}(\mu_1) + I_{t > t_D}(\mu_2 \bullet \Delta P \bullet u(t) \bullet dt) + u(t) \bullet dW$	-88.11	-102.58

Table S9. Summary of the DDMs used to model participants' choice behaviour in the absence of congruency component. Goodness-of-fits are reported through negative log-likelihoods (nLL) and Bayesian information criteria (BIC). [back to Results]

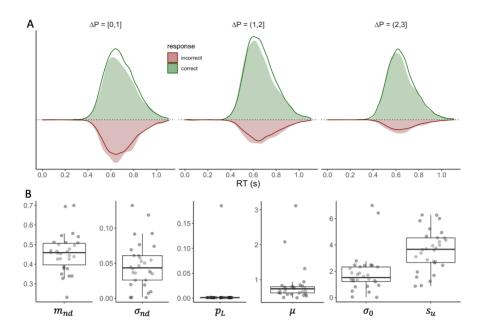


Figure S10. Participants' choice behaviour in the absence of congruency component cannot be fitted by a classical drift-diffusion model. A. Density distributions of observed (filled shapes) and predicted RTs (lines) extracted from the model with the highest goodness-of-fit, depending on the response accuracy (correct or incorrect) and the price difference between the two items (ΔP in euros). B. Distributions of the six fitted parameters, boxplots represent the 1st and 3rd quartiles of the data distribution, with thicker horizontal black lines corresponding to medians and whiskers extended to the largest value no further than 1.5 times the inter-quartile range (IQR). Behind is plotted individual data (N=30). [back to Results]

Sequential biases are independent of the objective evidence

The response deadline in the experiment put time pressure on participants. We wondered whether such urgency elicited the occurrence of sequential biases. As the experiment was not designed to look at sequential effects, we focused our exploratory analysis on whether participants responses, especially the faster ones, are biased by their directly preceding response. We classified trials as 'repeat' when the response (left or right) in the current trial was the same as the one in the previous trial, and as 'switch' when it was different. We found that faster choices were significantly biased toward switching compared to repeating $(V_{31} = 70, p = 2.37 \times 10^{-4})$, which was not the case for slower choices $(t_{31} = 1.22, p = .23)$. Especially, we observed that this 'switch' bias was present independently of the objective evidence present (ΔP small: $t_{31} = -2.51, p = .018, \text{ medium: } V_{31} = 65, p = 5.93 \times 10^{-4},$ large: $t_{31} = -3.75$, $p = 7.49 \times 10^{-4}$; Figure S11), suggesting that this bias serves as an initial adaptation to counteract the response urgency rather that an adaptive strategy to the trial's difficulty. However, accuracy didn't seem to be affected by this motor sequential bias as the probability to be correct was not significantly different between switch and repeat fast trials overall $(t_{31} = .61, p = .55)$ and inside ΔP conditions (small: $t_{31} = .99$, p = .33, medium: $t_{31} = 1.09$, p = .29, large: $V_{31} = 332$, p = .10).

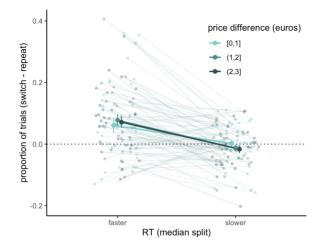


Figure S11. Fast choices are biased towards switching, regardless of the choice difficulty. Differences in the proportion of switch and repeat trials depending on the response time (faster or slower based on median splits) and the price difference (ΔP). Switch trials correspond to trials where the response (left or right) differs from the previous response, in opposite to repeat trials where the same response as in the previous trial is repeated. Darker colour dots represent group average and vertical bars the s.e.m. Lighter dots correspond to individual data and are connected with grey lines. [back to Results]

3. Chapter II. BALANCE BETWEEN BREADTH AND DEPTH IN HUMAN MANY-ALTERNATIVE DECISIONS

Alice Vidal, Salvador Soto-Faraco & Rubén Moreno-Bote (2022) **Balance between breadth and depth in human many**alternative decisions. *eLife* <u>11:e76985</u>

4. Chapter III. HUMANS ADAPT CHOICE VARIABILITY BEYOND REWARD MAXIMISATION IN SEQUENTIAL, MANY-ALTERNATIVE DECISIONS WITH LIMITED RESOURCES

Alice Vidal, Francesco Damiani, Alireza Vaylan, Salvador Soto-Faraco & Rubén Moreno-Bote (2023) Humans adapt choice variability beyond reward maximisation in sequential, many-alternative decisions with limited resources. *PsyArXiv* <u>https://doi.org/10.31234/osf.io/vfekr</u> Humans adapt choice variability beyond reward maximisation in sequential, many-alternative decisions with limited resources

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Abstract

Humans are strategic animals. We constantly make prospective choices, allocating limited resources in situations of uncertain, future outcomes. The management of our finite monthly budget, financial investments, or the allocation of time to the different questions in an exam are just a few examples. In these scenarios, both decision-making and resource allocation tend to fluctuate over time even under invariable set of constraints. However, it is unclear whether these fluctuations affect performance and whether they underlie additional objectives beyond pure reward maximisation. We address these questions using the breadth-depth dilemma, a novel ecological protocol where participants engage in sequential multiple-choice scenarios characterised by limited capacity. We designed two experimental environments. In one environment, optimal performance, formalised with an ideal allocator model, is associated with homogeneous resource allocation across consecutive choices. In contrast, the other environment entails that fluctuating resource allocation leads to greater expected rewards. Our study evaluates participants' adherence to these scenarios and measures fluctuations as deviation from homogeneous allocations. The results revealed that participants' behaviour fluctuates more than optimal, but critically, behavioural fluctuations adapt to the available capacity and the environmental context. Moreover, our findings unveil pronounced sequential strategies, such as save-forlater and reward history-dependent choice, further implying that these strategies contribute to decision variability. An extension of the optimal allocator model showed that the characteristic excess fluctuation is driven by entropy seeking, the pursuit of informationgain and risk avoidance. Although having a modest impact on performance, these strategies may reflect advantageous behaviours in the long run under ever changing real-world environments.

Highlights

- Within each choice, humans allocate capacity across a closeto-optimal number of alternatives, adapting to both the available capacity and the environmental context (Breadth-Depth trade-off).
- When allocating finite search capacity across sequential many-alternatives choices, humans fluctuate more than predicted by an ideal allocator model maximising immediate reward.
- These fluctuations present a structure underlying intended strategies like "save-for-later" and "reward history-dependent choice" and serve goals beyond return maximization: entropy seeking, information gain and risk avoidance.
- These strategies, while modestly impacting immediate performance, may have advantages in adapting to dynamic real-world environments.

Introduction

Ongoing behaviour is a highly dynamic and variable process, shaped by a multitude of internal and external factors. For example, the choice of words to express the very same idea may completely change. As a result, we can easily detect when someone delivers a rehearsed talk, highlighting the natural fluctuations that characterise spontaneous speech. This inherent variability extends beyond mere linguistic expression; it is a fundamental aspect of human behaviour that cannot be reconciled through numerous repetitions of the same action or controlled experimental settings (Rahnev & Denison, 2018; Renart & Machens, 2014). Confronted with the same decision multiple times, we might undergo different internal processes each time, consider information differently and eventually make slightly different choices. Spontaneous behavioural variability has been widely observed in motor outputs (Schmidt et al., 1979), even among professional athletes executing the same movements repeatedly (Bartlett et al., 2007; Menayo et al., 2012). Fluctuations have also been evident in vigilance (Davies, 1982; Fruhstorfer & Bergström, 1969) and sustained attention (Parasuraman, 1984), where humans naturally oscillate between task-related and taskunrelated thoughts (M. R. Cohen & Maunsell, 2011; Rapport et al., 2009; Sonuga-Barke & Castellanos, 2007), often engaging in mindwandering (Christoff et al., 2016; Killingsworth & Gilbert, 2010). Variability in behaviour is further noted in perception, where ambiguous stimuli may induce multistability, with several interpretations alternating over time (Attneave, 1971). This phenomenon might itself driven by stochastic neural variability (Gigante et al., 2009; Moreno-Bote et al., 2007) and the engagement of heightened top-down activity (Wang et al., 2013). However, even clear visual stimuli repeatedly presented may be perceived differently (Sergent et al., 2005). Momentary attentional disengagements from the ongoing task may actually be responsible for lapses in performance observed, for example, in continuous perceptual categorisation (Brink et al., 2016; Esterman et al., 2013) and working memory tasks (Aly & Turk-Browne, 2017; deBettencourt et al., 2019). Value-based decisions (Drugowitsch et al., 2016; Polanía et al., 2019) and economic games (Safra et al., 2022) are no exceptions and also exhibit spontaneous trial-to-trial variability. Additionally, smooth fluctuations in behaviour and performance can arise due to resource constraints, particularly in situations such as fatigue or extended time-on-task (Mackworth, 1948), where individuals might be disinclined to allocate substantial mental or physical resources due to a lack of motivation (Cerasoli et al., 2014; Zelick, 2007).

However, the impact of behavioural fluctuations on performance and their underlying objectives remain poorly understood. Extended literature delves into the neural origins of these pervasive behavioural variations. Research indicates that inherent fluctuations in brain activity contribute to variability in various cognitive processes, including attention (Kucyi et al., 2017; Smallwood & Schooler, 2006), perception (Boly et al., 2007; Ress & Heeger, 2003; Torralba Cuello et al., 2022; VanRullen, 2016), working memory (Wagner et al., 1998), and decision-making (Pessoa & Padmala, 2005; Mochol et al., 2021; Smith & Ratcliff, 2004; Drugowitsch et al., 2012, 2016; Findling et al., 2019).

Despite the extensive literature addressing behavioural fluctuations and their immediate causes, the extent to which these fluctuations ultimately enhance or hinder performance overall, and if they are aligned with underlying strategies, remains mostly unknown. Indeed, while behavioural variability can indeed arise from stochasticity in neural processes (Moreno-Bote, 2014), it should not be merely dismissed as noise (Garrett et al., 2013), as it may serve purposes beyond the sole maximisation of immediate reward (von Neumann & Morgenstern, 1944). In motor actions, while inherent noise within the nervous system was once considered the primary source of variability (Faisal et al., 2008; Osborne et al., 2005), recent research has highlighted its role in motor learning (Dhawale et al., 2017), revealing a significant connection between variability and skill acquisition (Sternad, 2018). Recent studies have also started to uncover the neural basis of curiosity (Kidd & Hayden, 2015) and have shown that monkeys are willing to trade rewards for advance information about gambling outcomes (Blanchard et al., 2015), suggesting the intrinsic potential of information seeking in guiding behaviour. An additional strand of literature shows that lapses in perceptual choices in mice reflect exploration (Pisupati et al., 2021), while humans adapt the balance between exploration and exploration based on the associated cost-benefit structure (J. D. Cohen et al., 2007a). What is more, the weight of exploration in behaviour is enhanced in extended time horizons, affording more opportunities to leverage newly acquired knowledge (Carstensen et al., 1999; Wilson et al., 2014) which underscores the interconnection between planning and information-seeking (Hunt et al., 2021). Finally, a recent study revealed that the ongoing fluctuations of dopamine contribute to structure spontaneous behaviour in mice (Markowitz et al., 2023), suggesting that variability plays an intrinsic role in organising behaviour even beyond goal-oriented tasks.

Collectively, these findings suggest that behavioural fluctuations may not be just the consequence of noise, but reflect the deployment of intentional strategies. This is substantiated by recent studies showing that humans exhibit deliberate adjustments in sensory evidence accumulation, favouring alternatives that maximise rewards (Kloosterman et al., 2019). Moreover, individuals adapt their learning rates based on the perceived value of information, indicating a purposeful adaptation to the informational context (Lee et al., 2023). In both cases, these adaptive alterations made over time introduce variability in behaviour. Additionally, the generation of novel and unexpected intentional behaviours, observed in animals, serves specific purposes. For instance, in the face of imminent threats, animals intentionally produce unexpected behaviours to evade predators (Evans et al., 2019). This intentional variability also contribute significantly to cognitive flexibility (Dajani & Uddin, 2015; Uddin, 2021), enhancing creative thinking and problem-solving abilities. Research further demonstrates that humans can purposefully engage in mind-wandering during task performance (Seli et al., 2016), which, despite potential performance lapses, fosters creativity,

advantageous in numerous contexts (Mooneyham & Schooler, 2013).

In this study, the aim is to investigate the relationship between behavioural variability and performance, exploring the potential that variability may be partially deliberate, contributing to objectives beyond mere reward maximisation. To do so, we use an extension of the breadth-depth (BD) dilemma. While the control of cognitive factors like attention and motivation is inherently challenging, this framework offers the distinct advantage of allowing for the experimental parametrisation of the decision maker's search capacity. Moreover, it formally delineates optimal solutions, providing clear insights into how these limited resources should be strategically allocated among multiple alternatives to maximise expected rewards (Moreno-Bote et al., 2020). The BD trade-off is applicable to various situations where search capacity must be allocated in advance before accessing the collected information. This dilemma formalises a very common problem of many realworld contexts, for example when planning a vacation, investing money, or shopping at a new local market. Consider this last scenario, products cannot (usually) be consumed on-site, and one must purchase fruits and vegetables before trying them out. Individuals face a choice: they can either buy numerous products from a few vendors to obtain a precise estimation of product quality from that one vendor (depth) or opt to purchase a few products from many different vendors (breadth), thereby increasing the likelihood of finding a good-quality vendor but at the cost of maybe not being able to identify the best one. Studies have demonstrated that humans tend to act in a manner close to optimal in this problem. They efficiently gather information to select alternatives associated with higher payoffs and adapt their strategy based on the richness of the environmental context (Vidal et al., 2022). This framework provides therefore an excellent basis for investigating whether this efficient balance between breadth and depth is sensitive to variability in the resource allocation or remains stable, and how it relates to performance. Furthermore, by allocating a restricted resource budget across various choices instead of a single choice,

our paradigm enables a more active information search where participants can decide not only what to sample but also in which extend. Additionally, the BD dilemma has the advantage, compared to the well-known exploration-exploitation dilemma (Berger-Tal et al., 2014), of having an easily tractable optimal solution, particularly when dealing with numerous alternatives, as is often the case in real-life scenarios. Moreover, while in the EE dilemma, seeking new information through exploration comes at the cost of renouncing to exploit the currently rewarding alternative, such trade-off is absent in the BD and enables to better focus on information seeking strategies. Finally, although the ideal observer considers each choice as independent of each other, this framework enables the characterisation of anticipated strategies in resource allocation. Planned sampled strategies are therefore in larger extent detangled from the environment volatility and more accessible than in the EE dilemma.

As a result, the BD dilemma, an ecological decision-making paradigm featuring multiple alternatives, boasts distinctive features: a controlled search capacity and accessible optimal strategies adhered to by humans. Utilising this framework, our study intends to fill the gap between the dynamic nature of human choices, sometimes perceived as random noise, and the underlying goals that may be embedded within them. Specifically, we aim to investigate the existence of fluctuations in the allocation of limited resources during information gathering. We implemented two environmental contexts in which variability in the resource allocation is either optimal, or in contrast should be avoided. By decoupling fluctuations from expected performance, we aim to identify potential underlying cognitive processes driving behavioural variability. Disentangling variability in information sampling due to boredom (and task disengagement) from intentionally planned strategies can be challenging. To this end, we investigate how fluctuations change in response to variations in the reward structure of the context. We hypothesise that when gathering information, humans are not purely reward maximisers; instead, they sacrifice optimality to seek valuable information to facilitate future decisions

and explore possible existing strategies while considering the level of risk and uncertainty one can afford.

We first examine how participants manage finite search resources (capacity) across various alternatives within a choice (breadth-depth trade-off) depending on the probability of success of the alternatives (environment richness), and look to replicate previous findings (Vidal 2022). Subsequently, we delve into an exploration of how experimental conditions, including the number of consecutive choices (horizon) and the total number of resources accessible in the block, influence this BD trade-off.

Our focus then shifts towards participants' resource allocation across successive choices: are finite resources distributed uniformly among the choices or exhibit fluctuations? According to the optimal model, we anticipate observing more pronounced fluctuations when limited capacity is available in the poor environment, when most of the alternatives have low probably of success. Conversely, we expect resources to be evenly distributed among choices in all the other experimental contexts. Our observations reveal that participants exhibit fluctuations that surpass the optimal predictions. Building on prior literature, we also hypothesise that participants are likely to exhibit heightened fluctuations in blocks with extended horizons. Furthermore, we explore the specific contexts in which these fluctuations transpire, considering factors such as available capacity, previous and future resource allocation and reward history. In the final part of our study, we extend the optimal model to investigate the potential presence of underlying strategies, entropy seeking from the maximum occupancy principle (Ramírez-Ruiz et al., 2022), risk aversion (Tulloch et al., 2015) and the pursuit of relevant information (Gottlieb, 2012), that elucidate the intentionality behind the observed increased variability.

Results

Humans follow a stable close-to-optimal Breadth-Depth trade-off adapted to the environment richness.

We extended the BD Apricot task (Vidal et al., 2022) in a novel way to investigate how humans forage for information by allocating a limited amount of resources over consecutive multiple choices, with the goal to accumulate rewards in uncertain environments. Participants engaged in a gamified version of the foraging task, where they purchase apricots in bulk from one out of twenty unknown suppliers (video of the experimental design available here). Different suppliers vary in the proportion of good quality apricots they serve. The objective was to maximise the number of good-quality apricots purchased throughout the experiment, by developing an efficient and informative sampling strategy. For sampling, participants were provided with a budget of coins to be spent in buying sample apricots from suppliers. This budget is characterised by a fixed number of coins N_c which represents the initial capacity of a block. Since each block could have a different number of trials $(N_{trials} = \{10, 20\}, \text{ block length})$, we introduced the capacity ratio r, which is defined by the average capacity available in a trial $(r = N_c/N_{trials})$. For instance, in a block with a capacity ratio r of 2 and length of 10 trials, a total of 20 coins were initially given (Figure 1A). When characterising the available capacity in a block, we refer to this relative value r instead of the initial capacity N_c because we are considering block of different lengths. In each trial, participants could decide how many coins they would use to gather information about the suppliers (Figure 1B – sampled trial), or forgo sampling to save coins and randomly select one supplier (Figure 1B – skipped trial) for the final purchase of 100 apricots (Figure 1B-d) at the end of each trial. Participants were encouraged to use all their available coins within the block (any remaining coins were forfeited, as they could not be carried over to the next block). The allocated capacity in the trial n (n={1, 2, ..., N_{trials} }) denoted as C_n ($C_n = \{0, 1, 2, ..., N_r\}$), where N_r is the remaining capacity at that trial ($N_r = N_c - \sum_{i=1}^{r-1} C_i$). We refer generically to C as the allocated capacity in a given trial within a block. When sampling, participants used each coin to buy one sample apricot from a chosen supplier, and they could purchase multiple sample apricots from the same supplier to obtain a more accurate estimation of its probability of providing good-quality apricots. At any time, participants had the choice to stop sampling by double clicking on the sample situated at the centre (Figure 1B-b) and then the quality of the sample apricots would be revealed (good: orange or bad: purple; Figure 1B-c). The feedback regarding the sampled alternatives was consequently postponed until after the termination of the sampling, thereby preventing any real-time adjustment or correction of the search strategy. The final bulk purchase had then to be made by choosing from one of the sampled suppliers, therefore completing the trial and proceeding to the next, or to the end of the block.

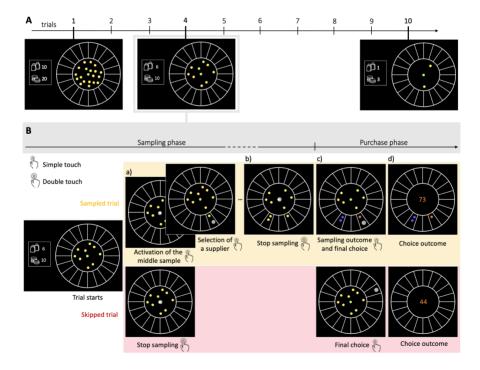


Figure 1. The BD apricot task with capacity freely allocated amongst trials (the free BD apricot task). A. Example of one block composed of 10 consecutive choices (trials, $N_{trials} = 10$) and with an initial capacity N_c

of 20 samples. The capacity ratio r of this block represents the initial number of samples divided by the number of trials, in this case r=2. On each trial, the remaining coins are displayed at any time in two ways: written on the left of the wheel (bottom number) and materialised by the vellow and green dots located within the centre of the wheel. For example, at the beginning of the 4th and last trial, the remaining capacity (N_{r}) is respectively of 10 and 3 samples. The remaining number of purchases (trials) in the block is also constantly displayed on the left of the wheel (top number). B. Example of one trial. Participants allocate a limited search capacity (coins) to assess the quality of good apricots in different suppliers (sampling phase). Subsequently, they make a final purchase of 100 apricots from one of the sampled suppliers (purchase phase). Each distinct black section of the wheel represents a different supplier. The initial number of coins per block varies pseudo-randomly from block to block within a finite range (defined by the capacity ratio r, multiplied by the number of trials in the block N_{trials} - see Methods). To allocate the coins to suppliers, participants have first to click on the designated active coin displayed at the centre (green dot) and then select the supplier to sample from (panels a) –both touch screen events are indicated by a large grev dot. One of the inactive (vellow) coins is then automatically activated and displayed, in green, at the centre. This sequence repeats until all coins are allocated or until participants end the sampling phase by touching twice the centre coin (panel b). Then, each of the allocated samples turn either orange, representing a good-quality apricot, or purple, representing a bad-quality apricot (panel c). Finally, after this information is revealed, the participant selects one of the sampled suppliers for the final purchase of 100 apricots (with a touch screen, indicated by a large grey dot) and the choice outcome is immediately displayed (panel d). In the case where no coin has been allocated (skipped trial – lower panels), participants select randomly one of the 20 suppliers for the final purchase.

Participants were immersed in either a rich or in a poor environment, where each supplier had an independent proportion of good quality apricots defined by beta distributions (prior means in the poor environment: .25, and in rich: .75, see Methods. The optimal sampling strategy, aimed at maximising the expected return, emerged from a trade-off between sampling many alternatives with little precision (breadth) or fewer alternatives with higher precision but with the risk not to have any satisfactory option (depth). At fixed capacity this balance varied depending on environment richness, depth being favoured in environments where the overall probability of success of the alternatives was higher (Figure 2A). Indeed, in the rich environment, where a majority of suppliers sold good quality apricots in high proportions, it was relatively easy to identify a good supplier and thus, did not require investing significant sampling capacity per trial. Using Monte-Carlo simulations, we find that the optimal strategy (the strategy of an ideal allocator with perfect memory) is to sample all trials with a capacity equal to the block's capacity ratio (r, either 2, 3, or 4), thus avoiding skipping any trial (Figure 2C-D right panels, see Methods for more details). In contrast, the poor environment had a higher proportion of low-quality suppliers, making it more challenging to find a reliable provider. In such situations, achieving informative sampling, for example observing at least one sampled apricot of good quality, was crucial to identify an above-average supplier. We find that, in this case, the optimal strategy is to allocate a minimum of three samples when the available capacity in the block is small (r=2), distributing them across the maximum number of trials and skipping the remaining ones (Figure 2C-D left panels).

The primary focus of this study is to investigate whether individuals are capable of developing strategies that closely approach optimality in the way they distribute their limited capacity across consecutive choices. Previous research has found that, in addition to pursue reward maximisation, sampling strategies may seek novel information, are influenced by random exploration processes and individuals' attitudes towards uncertainty (Daw et al., 2006; J. D. Cohen et al., 2007a; Gottlieb, 2012; Lee et al., 2023). Here we aim to investigate the presence of such systematic deviations in an information search task (free Apricot BD) with limited parametrised capacity and detangle their underlying causes. According to the ideal allocator, fluctuations in capacity allocation from one choice to another are expected to be stronger in poor environments compared to richer ones. Our experimental design also included variations in block length, with either 10 or 20 trials (that is, cycles of suppliers sampling and final purchase) under a single budget. Based on previous literature (Carstensen et al., 1999) and although not predicted by the ideal allocator, we anticipate that the block length will impact how individuals manage their capacity over time,

with longer horizons encouraging more exploration and, consequently, larger fluctuations in the allocation of resources.

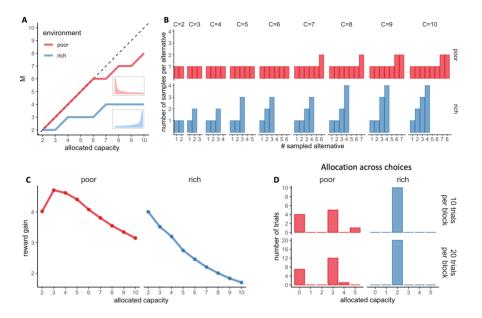


Figure 2. Optimal allocations of search capacity. A. Optimal Breadth-Depth trade-offs: number of alternatives sampled (M) maximising the expected reward depending on the capacity allocated in the trial and the environment richness (colours). Dashed lines indicate unit slope line. Prior distributions of success (proportion of good quality apricots) of each environment are plotted next to each curve. **B.** Number of samples allocated to each sampled alternative maximising the expected reward (optimal), depending on the capacity allocated C and the environment richness (colours). **C.** Distribution of the difference in reward expected when sampling with capacities from 2 to 10 (assuming an optimal BD trade-off) and when choosing randomly divided by the allocated capacity (reward gain), for each environment. **D.** Optimal distribution of trials depending on their sampling capacity, the block size and the environment richness for a capacity ratio r of 2.

First, we focused our analysis on the *Breadth-Depth* trade-off, which refers, in each trial, to the number of alternatives sampled (M) as a function of the capacity allocated within the trial (C). Allocating few samples to many different suppliers would be considered as *Breadth* behaviour (for example, when M=6 suppliers are sample with a total C=6 coins), whilst allocating many samples

in few suppliers is considered as *Depth* (for example, when M=1) supplier is sample with C=6 coins). In line with previous theoretical (Moreno-Bote et al., 2020) and experimental findings (Vidal et al., 2022). we observed that the number of alternatives sampled varied with both the capacity allocated and the environment richness in close-to-optimal manners (Figure 3). At lower capacities, participants sampled as many alternatives as possible, following a pure-breadth strategy. As more capacity C was allocated, participants tended to focus more capacity on few alternatives. As previously reported (Vidal et al., 2022), this BD trade-off was best captured using the free-power model $(R_{adi}^2 = .97 \pm .03)$ than a linear model $(R_{adj}^2 = .96 \pm .04)$ (paired Wilcoxon test, V = 112, p = .0016) and the optimal piece-wise power law model (all ANOVAs not significant, for $\alpha < .05$). We also replicated previous findings (Vidal et al., 2022) showing that environment richness promotes depth over breadth (power exponents: $a_{noor} = .95 \pm .08, a_{rich} = .76 \pm .15$ (Wilcoxon test, W = 61, $p = 7.94 \times 10^{-5}$, Figure 3A). We compared these exponents with the ones obtained by fitting the optimal values of M with the powerlaw model (poor: .99±.02, rich: .73±.03) and didn't find any significant difference in the poor (paired Wilcoxon test, V = 47, p = .10) or in the rich environment (paired t-test, $t_{19} = .90, p = .38$), suggesting that overall, participants allocated capacity amongst an optimal number of alternatives. These findings differ to previously published results, using a design where the number of samples to be allocated per trial was fixed, showing that people are slightly sub-optimal at balancing breadth and depth (Vidal et al., 2022). Even though, sampling strategies from both studies cannot be formally compared due to different capacities used, they raise the idea that more freedom in search strategy may stimulate performance. We come back to this point in the discussion

Even though environment richness had a clear impact on the participants' BD trade-off, initial capacity in the block (N_c) did not. Indeed, on one hand, block length did not have a significant effect on the power exponents (permutation ANOVA, p = .94) and neither interacted with the environment (p = .59, Figure 3B, $a_{poor,10} = .95 \pm .09$, $a_{poor,20} = .95 \pm .08$, $a_{rich,10} = .78 \pm .16$, $a_{rich,20} = .75 \pm .15$). The difference between the power exponents in the short and long block was significantly smaller than .1 (paired TOST test, $t_{39} = -5.30$, $p = 2.43 \times 10^{-6}$), and therefore negligible. On the other hand, capacity ratio r did not have a significant effect on M (permutation ANOVA, p = .60, Figure 3C), neither interactions between r and allocated capacity C (p = .93), or between r and environment richness (p = .95) were significant. These results suggest that participants follow a balance between breadth and depth adapted to the environment but stable across capacity available and the horizon, meaning that the allocation strategy exclusively depends on the number of allocated samples on each trial and the environment richness.

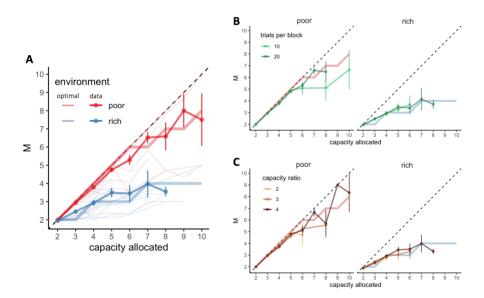


Figure 3. BD trade-offs are close-to-optimal and adapt to the environment, while being stable among blocks with different length and capacity ratio. A. Number of alternatives sampled (M) depending on the capacity allocated and the environment richness (colours). Group average and s.e.m. are plotted above individual data (thin light lines) and optimal values of M (thick light lines). Dashed lines indicate unit slope line. B-C. Colours represent the block length (B) or the capacity ratio r (C). N=20 per environment.

Humans' allocation capacity fluctuates more than optimal

Optimal allocation (Moreno-Bote et al., 2020) predicts that, inside a block, the resources should be homogeneously distributed amongst the trials and equal to the capacity ratio (r), except in the poor environment when the ratio is small (r=2). Indeed, allocating two samples is not sufficient to gain a useful information, then, a capacity of 3 coins (samples) should be allocated in as many trials as possible (Figure 2C), which necessarily implies that some trials should be skipped (no coins assigned, and left to random choice). In this case, fluctuating is optimal: namely, allocating different capacity across trials of the same block. To formalise this, we considered as fluctuations the trials for which the number of allocated resources is different from the capacity ratio of the block $(C \neq r,$ Figure 4A). Overall, we found larger fluctuations than what would be predicted by an optimal allocation strategy (mean±sd proportion of trial with $C \neq r$: .40±.28, Wilcoxon test, V = 694.5, $p = 2.21 \times 10^{-15}$, Figure 4B).

We observed that these fluctuations corresponded to two strategies: skipping a trial (no resources allocated, Figure 4A – light purple) or spending a capacity inferior to the ratio, 0<C<r, defined as 'under-sampling' (Figure 4A – dark purple). While the first was predicted by the optimal allocator (at least in poor environments with r=2), the latter wasn't. In line with the optimal strategy, we found that when available resources are scarce (low r), allocation fluctuates more from trial to trial. This leads to more skipped trials than in higher capacity ratio conditions (F=46.07, p<4.2 $\times 10^{-8}$, Figure 4C), a strategy that allows more extensive search on the remaining trials. However, contrary to what predicted by the optimal model, we didn't observe significantly more skipped trials in the poor compared to the rich environment for block with a capacity ratio of two (poor: 23.3±19.9%, rich: 17.8±16.7%, W=168, p=.39, Figure 4C). Finally, fluctuations are amplified in longer blocks (V=4257, p= 2.13×10^{-15} , Figure 4C - colours), which had a significantly higher proportion of skipped trials than optimal, suggesting that participants might capitalise on the larger available resources to increase exploration.

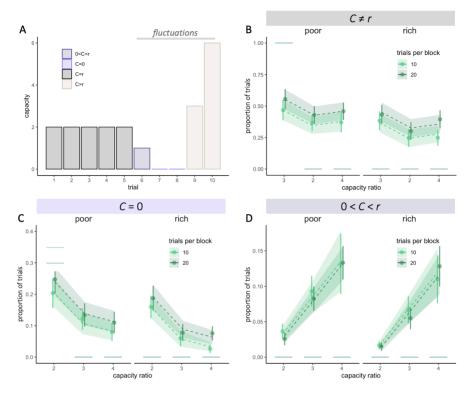


Figure 4. Participants capacity allocation fluctuates more when little capacity is available and with larger horizons. A. Example of capacity allocation from one participant throughout consecutive trials in a block of length 10 and ratio r=2. B-D. Fluctuations are defined as trials for which the allocated capacity C is different from r. Observed averaged proportions of trials (dots) where $C \neq r$ (fluctuations - B), C=0 (skipped trials - C) and 0 < C < r (D), depending on the capacity ratio r, block length (colours) and the environment (poor or rich). Vertical bars represent s.e.m. of the data, while dashed lines and shaded areas represent respectively the predicted averages and s.e.m. using LMEM. Horizontal segments represent the proportion of each type of trials predicted by the optimal model.

Participants also chose to allocate some resources but less than the capacity ratio on a significant number of trials (7.46±7.13%, $V = 780, p = 5.44 \times 10^{-8}$, Figure 4D), which was not predicted by the optimal model. These fluctuations increase with the capacity ratio (LMEM, $F_2 = 45.19, p < 2 \times 10^{-16}$) but were not affected by the block length ($F_1 = .08, p = .78$) and the environment richness ($F_1 = .68, p = .42$). Such fluctuations may reflect a balance

between selectively gathering more information in some trials (C>r) whilst trying to avoid skipping trials (and leaving the final choice to chance).

Overall, these deviations from optimality had little impact on performance (mean±sd: -3.07±4.81%), but the more the proportion of fluctuations diverged from the one predicted by the optimal model and the greater was the loss in outcome. Indeed, our observations indicate that in the poor environment, the relationship between participants' average outcomes and their level of fluctuations (trials with $C \neq r$) was best captured by a second-order polynomial regression $(R_{adj}^2 = .26, p = .029)$ as opposed to a linear regression ($R_{adi}^2 = .12$, p = .078) (Figure S4 – left). In fact, participants achieved highest average outcomes when their resource allocation among choices approximated the predicted optimal pattern of 1/3rd (see Figure 2D). In the rich environment, as predicted, the association between participants' average outcomes and fluctuations was more accurately captured by a linear regression $(R_{adi}^2 = .15, p = .053)$, than by a second-order polynomial regression $(R_{adi}^2 = .12, p = .13)$ (Figure S4 – right). In this case, higher outcomes were achieved when fluctuations were lowest (at 0). This finding confirmed that a more uniform allocation of resources among choices tended to produce higher outcomes in rich environments. These results are crucial as they confirm that the experimental design influenced participants' outcomes as anticipated, potentially shaping their strategies to align with the ideal allocator model.

Evidence for an intentional strategy

We then investigated the origin of the observed fluctuations beyond those predicted. One possibility is that they resulted from an exhaustion of resources given the allocation policy over the initial part of the block, leading participants to obligatorily skip or underspend in the remaining last trials. Another possibility is that the decision of skipping trials was intentional, meaning that they had enough resources to sample the trial but decided not to do so. We observed that the great majority of trials with no allocated capacity (skipped) (mean±s.d. across participants: $82\pm31\%$ and overall: 84%) occurred while some capacity is remaining ($N_r \neq 0$), and therefore intentionally, suggesting the possibility that participants may be saving resources for later.

Indeed, participants allocated significantly more resources in trials directly following trials with low capacity allocations (e.g., fewer capacity than the ratio; C < r) compared to trials directly preceding them (LMEM, $\chi_1^2 = 16.24$, $p = 5.58 \times 10^{-5}$, Figure 5), suggesting that overall, allocating little capacity is part of an anticipatory strategy to explore further later. This effect didn't interact with either the capacity ratio ($\chi_2^2 = .69$, p = .71), nor the block length ($\chi_1^2 = .81$, p = .37).

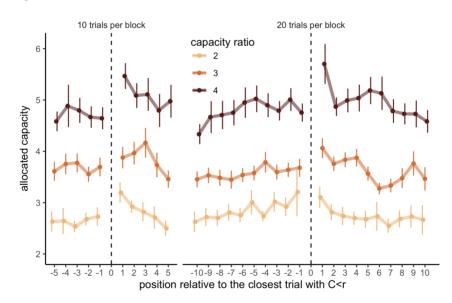


Figure 5. Allocating fewer capacity than the ratio is part of an anticipated strategy for sampling more in the next trial. Capacity allocated in trials depending on their relative position to the closest trial with an allocated capacity inferior to the capacity ratio of the block (C < r), depending on the block length (left: 10 trials, right: 20 trials) and the capacity ratio (colours). Each data point represents the average of 12 to 37 participants with at least 3 data points per participant. Vertical bars represent s.e.m.

Participants adapt their sampling strategy to the choice outcome.

In the earlier analysis we observed that participants adapted their sampling strategy to the limited capacity available, and prioritised spending little to no capacity in order to spend more later (Figure 5). Next, we addressed whether participants also adapted their strategy according to the outcome received in a given trial. To explore that, we divided trials as a function of the outcome received (median split), separately for sampled and skipped trials. The results revealed that participants are more likely to switch strategy (sampling after skipping, or vice versa) following low outcome trials $(.14\pm.13)$ compared to high outcome ones $(.10\pm.12)$ (Wilcoxon test, V = 504, $p = 6.76 \times 10^{-5}$, Figure 6A). The magnitude of this effect was not affected by the trial type (sampled or skipped, F = 1.78, p = .20) nor the environment richness (permutation ANOVA, F = 3.85, p = .061), although we found a significant interaction between the environment richness and trial type (F = 6.91, p = .012). Post-hoc analyses revealed that the higher probability to switch strategy is only found following sampled trials in the poor environment ($V = 93, p_{adj} = .034$; after skipped trial: $t_{13} = -.03$, $p_{adi} = 1$, Figure 6B - left), while in the rich environment this effect is found solely after skipped trials $(t_{11} = 2.17, p_{adj} = .042, \text{ after sampled trial: } V = 66, p_{adj} = .14,$ Figure 6B - right). Although these results have to be interpreted with caution due to the limited sample size included, they suggest that participants consider differently the outcome received depending on the environment richness. In the rich environment, high outcomes are easily obtained and expected even when choosing randomly a supplier (skipped trial), therefore receiving a low outcome may be more surprising and enforce a switch in strategy for sampling. In contrast, in the poor environment, low outcomes are expected when skipping and it's not surprising that they don't affect participants' future strategy.

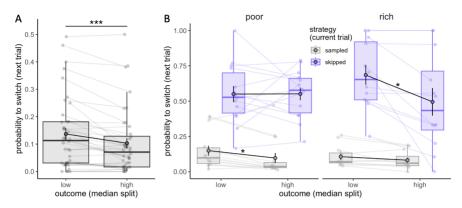


Figure 6. Participants adapt their sampling strategy to the outcome received. A-B. Probability to switch strategy in the next trial (from sampling to skipping and vice versa) depending on the outcome received (median split, calculated separately for individuals and skipped and sampled trials, N=40) (A) and the strategy in the current trial (sampling or skipping) as well as the environment (poor: N=14, rich: N=12) (B). Boxplots represent the 1st and 3rd quartiles of the data distribution, with thicker horizontal black lines corresponding to medians and whiskers extended to the largest value no further than 1.5 times the inter-quartile range (IQR). Lighter dots represent individual data and are connected with lighter lines, while group averages are plotted on top (colour dots circled in black) and connected by black lines. Vertical black bars represent s.e.m. '*': p_{adi} <0.05, '***': p <.001.

Identifying deviations from optimality observed in the resource allocation between choices.

We have observed that the way participants allocate their available resources amongst the consecutive choices differed greatly from the optimal model. However, the optimal model considers expected reward maximisation as the only goal. To better understand potential origins of participants performance deviations from optimality, we fitted in each block p_c , the observed probability to allocate a capacity *C* from 0 to 10, with an extension of the optimal model that considered that, in addition to maximising net reward, there is an intrinsic motivation for sampling with higher variability across trials (Eq.1 and Methods for more details).

(Eq.1)
$$EU = \sum_{c=0}^{10} R_c p_c + \alpha \sum_{c=0}^{10} I_c p_c - \beta p_0 + \gamma \left(-\sum_{c=0}^{10} p_c \log p_c \right)$$

Specifically, in addition to the expected reward for each capacity allocated R_c , the expected utility EU modelled here incorporates three additional factors that we hypothesised are influencing participants sampling behaviour. First, a factor related to information gain. We based this factor on findings suggesting that not only experienced, but also fictive rewards and valuable information about future outcomes have been found to be encoded in the brain (Bromberg-Martin & Hikosaka, 2009; Bromberg-Martin & Monosov, 2020; Hayden et al., 2009), establishing a framework for curiosity and explorative behaviours aimed at reducing uncertainty about the environment (Gottlieb, 2012). To accommodate this aspect, we introduced an information benefit I_c which can take different forms (see Methods for more details). Here we report models including the best fitting I_c , corresponding to the probability of observing a single highest sampled outcome (S_i) (see Figure S5). We hypothesise that participants may want to maximise this probability to later facilitate the selection of one out of the many sampled alternatives. Second, we incorporated factors related to individual traits. Individual features such as risk aversion have been demonstrated to influence the allocation of limited resources in various types of uncertain decisions (Chronopoulos et al., 2011; Dow & Werlang, 1992; Tulloch et al., 2015), suggesting that it might affect participants' propensity to skip a trial (p_0) and leave it to chance. Finally, participants sampling behaviour may be driven by a tendency to occupy action-state space (maximum occupancy principle), compelling them to try out various resources allocations and gain a global understanding of the environment (Ramírez-Ruiz et al., 2022). To model this, we introduced an entropy term. These three factors in the model were respectively weighted by parameters α , β and γ .

Participants sampling strategy incorporates exploration, individual risk aversion features, as well as information benefit.

We fitted, for each block, the probability to spend a certain capacity *C* in a trial with five different models including combinations of the optimal model with the three factors described above (see Figure S6 for the fits of all probabilities of capacity allocations). The results showed that the notable deviations from optimality observed in the empirical data, especially in the probability to skip a trial altogether (Figure 7A) and the probability of low capacity allocation (i.e., 0 <C < r) (Figure 7B), are well captured by the full model (including optimised α , β and γ parameters). We then fitted partial models excluding one of the three parameters (setting either α , β or γ equal to 0) to evaluate the importance of each of them in predicting the data. Looking at averaged AIC (Figure 7C) and BIC, we observed that in the rich environment, the full model is required to reproduce participants' sampling behaviour. Instead, in the poor environment a model including only exploration and risk aversion components $(\alpha = 0, \beta \neq 0, \gamma \neq 0)$ was sufficient to predict the data. Indeed, in the poor environment, the majority of the alternatives are associated with very low outcomes. Better alternatives are therefore easily detectable, which may explain that participants may focus on maximising the reward above and before the sampling information received. In contrast, in the rich environment, good alternatives are easy to find but one's need to rely on an efficient sampling to select the best alternative. These results are also in line with previous literature showing that the value of information increases when higher stakes are in play (Blanchard et al., 2015). Analyses of goodness-of-fit further demonstrated the significance of exploration in participants' sampling strategies, as models excluding this component ($\gamma=0$) performed poorly in predicting the data. Moreover, in the poor environment, although models with null values for either information benefit or risk aversion (either $\alpha=0$ or $\beta=0$) provided relatively good fits compared to the full model, the model without both ($\alpha=\beta=0$) resulted in significantly worse predictions, particularly concerning the proportion of skipped trials. This finding indicates that, in addition to maximising reward and

exploration, participants also adopt a sampling strategy that aims to minimise the uncertainty associated with skipping a trial.

Additionally, among of the three information benefits considered (see Methods), we found that the one providing the best fit to participants' sampling strategy is the model corresponding to the probability of having a unique sampled alternative with the highest observed sampled probability (number of positive samples out of the total number of samples allocated within this alternative) $(I_c = I_{single, c})$ (Figure S5). This information is likely to be highly valuable in guiding participants towards selecting one of the sampled alternatives for their final purchase and reducing the uncertainty associated with this choice, particularly in the rich environment where distinguishing the best alternative among many good ones may be more challenging.

Following the initial model selection, we analysed how the factors $(\alpha, \beta \text{ and } \gamma)$ estimated from the best fitting models changed with the experimental variables manipulated (Figure 7D). In both the rich and poor environments, we observed that β decreased with capacity ratio (poor: $\chi_1^2 = 102.01$, $p < 2.2 \times 10^{-16}$, rich: $\chi_1^2 = 12.15$, $p = 4.90 \times 10^{-4}$) and block length (poor: $\chi_1^2 = 7.51$, p = .0061, rich: $\chi_1^2 = 16.68$, $p = 4.43 \times 10^{-5}$), suggesting the more resources are available and the less participants are reluctant to skip sampling. While it might initially appear counterintuitive, given the lower frequency of skipped trials in blocks with larger capacity ratios, it aligns with the optimal model's predictions. As the capacity ratio grows, the model suggests that skipping a trial becomes less optimal, leading to an increase in the associated loss in expected reward. Consequently, although participants tend to skip fewer trials when the capacity ratio is larger, the model predicts a diminished level of risk aversion.

Additionally, we found that in the poor environment, where good alternatives are scarce, exploration may be accentuated as more resources are available, as suggested by the increase in γ with the capacity ratio ($\chi_1^2 = 7.06$, p = .0079). Such increase was not

found in the rich environment ($\chi_1^2 = .34, p = .56$), nor with the block length in any of the two environments (poor: $\chi_1^2 = .049, p = .82$, rich: $\chi_1^2 = .36, p = .55$). Finally, in the rich environment, we observed that α significantly decreases with the capacity ratio ($\chi_1^2 = 5.78, p = .016$) but not with the block length ($\chi_1^2 = .007, p = .93$), suggesting that participants look to maximise the information benefit when resource are scarce.

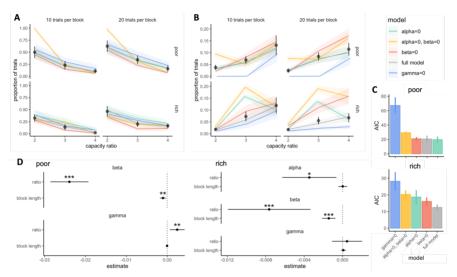


Figure 7. Participants sampling strategy considers exploration and individual risk aversion features. Proportion of skipped trials (C=0, A) and trials with a non-null capacity allocated inferior to the ratio (0 < C < r, B) depending on the capacity ratio, block length and environment richness. Black points represent the averaged observed probabilities across participants and vertical bars the s.e.m. Colours lines represent the averaged fitted probabilities for each model and the shaded areas the s.e.m. across participants. C. averaged AIC across participants in the poor (top) and rich (bottom) environment estimated by fitting the data within each block using the five different models. Vertical bars represent s.e.m. across participants. D. Factors (alpha=0' in the poor environment and 'full model' in the rich environment) regressed with the capacity ratio and block lengths using LMEM (bars represents 95% confidence intervals). '*': p < .05, '**': p < .01, '***': p < .001. N=20 in each environment.

Additionally, as a reality check, we fitted our data with the same models excluding the reward component ($R_c = 0$). As expected, these models systematically gave worst fits, suggesting that

participants are doing the task correctly and try to maximise the received outcomes.

In summary, these results illustrate that the deviations from optimality observed in participants' sampling behaviour are not a result of random decision processes, but rather stem from systematic heuristics that are integrated into a comprehensive strategy considering both overarching goals and individual characteristics.

Balancing under-sampling and skipping is explained by estimated level of risk aversion.

We further explored the strategies underlying fluctuations at the individual level and whether our extended model captures some of the differences between participants. First, we observed that for participants exhibiting significant fluctuations (at least 15% of the trials), allocating either no capacity or a capacity lower than the capacity ratio ('under-sampling': 0<C<r) in at least one trial per block on average, the more participants skipped sampling and the less they under-sampled (tau = -.46, p = .006, N=19) (Figure S8A). To control from spurious correlations computed on the same data set, we randomly split the 18 blocks in two subsets S (S={1,2}, balancing experimental conditions). We computed the average probabilities to skip $p_{skip, S}$ and to under-sample $p_{us, S}$ from each group and run Kendall correlations tests between $p_{skip, 1}$ and $p_{us, 2}$, and $p_{skip, 2}$ and $p_{us, 1}$. This method was repeated 100 times and led to on average 67% (95%CI: [60.0,73.5]) of the tests being significant (p<.05) which is significantly higher than the false positive rate α =.05 (Binomial test, $p < 2 \times 10^{-16}$). This intricate balance between these strategies, both contributing to fluctuations, is further linked to the estimated level of risk aversion (β extracted from the best fitting model in each environment). Specifically, strategies favouring skipped trials are associated with lower β values (LMEM: t = -11.72, $p < 2 \times 10^{-16}$), while under-sampling is linked to higher β values (t = 5.93, $p = 4.96 \times 10^{-9}$) (Figure S8B). In the same way as above, we controlled for dependencies between estimated β values and probabilities of skipping and under-sampling by correlating these values extracted from different subsets of our data (β_1 , β_2). For participants exhibiting significant fluctuations (at least 15% of the trials), results confirmed a negative correlation between β values and p_{skip} (proportions of significant tests: 100% [98.2,100], binomial test: $p < 2 \times 10^{-16}$) and a positive correlation between β values and p_{skip} (proportions of significant tests: 94% [89.8,96.9], binomial test: $p < 2 \times 10^{-16}$). These findings are noteworthy for delineating the underlying factors guiding participants' strategies, including individual differences related to risk tolerance.

Humans tend to sample the alternatives homogeneously.

The optimal model also predicts the allocation of resources among each sampled alternative that maximises the reward. Particularly in the rich environment, where depth is favoured over breadth, predictions indicate that as capacity increases, it is optimal to allocate a different number of samples to each sampled alternative, thus avoiding ties (Figure 8A, upper panel). However, previous research has indicated an opposing tendency among participants, who preferentially tend to allocate their resources homogeneously among the sampled alternatives (Vidal et al., 2022). In this study, we replicated these findings and observed that participants favoured homogeneous allocation of resources in both the rich (Figure 8A, lower panels) and poor environments (Figure S9), over and above what would be expected by an optimal model. To characterise this bias towards homogeneous sampling, we focused on trials where a pure breadth strategy is not optimal $(M_{opt} < C)$, indicating that homogeneous sampling is, therefore, suboptimal. Due to insufficient data to meet this condition in the poor environment, our analysis focused on the rich environment (see methods for more details). We computed the standard deviation of the ordered counts for each sample allocation, averaged for each participant, and compared it to the standard deviation of the optimal allocation. We observed that the standard deviation of sampled alternatives is significantly lower than that estimated from an optimal sample

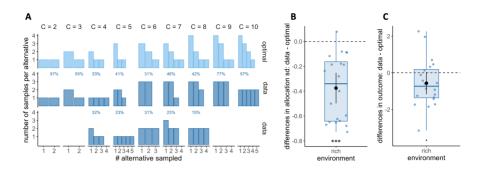


Figure 8. Participants have a tendency to homogeneously allocate capacity amongst the sampled alternatives, but it has little impact on the outcome. A. Number of samples allocated to each sampled alternative depending on the capacity allocated C in the rich environment. Upper panels: allocation of samples maximising the reward (optimal). Lower panels: most frequent allocations of samples observed across participants as a function of capacity. The allocations representing at least 50% of the trials are displayed and their likelihood is reported. **B.** Distribution of the differences between observed and optimal standard deviations of the distribution of samples among the selected alternatives in each environment (e.g. if C = 4 and 2 samples are allocated in a first alternative while the last 2 samples are each allocated in a second and third alternative, the standard deviation of this sample allocation would correspond to sd ($\{2, 1, 1\}$) ≈ 0.577). Note that more homogeneous distributions tend to lead to lower standard deviations. C. Distributions of the mean differences between observed and optimal outcomes in each environment. In the last two panels, dots represent participants and include all trials for which the optimal number of alternatives sampled doesn't reflect a pure breadth strategy ($M_{opt} < C$ - see Materials and methods for more details) and a capacity allocated up to 10. Below each distribution are presented results of one-sample Wilcoxon test ('***': p <0.001 - B) and one-sample t-test ('.': p < 0.10 - C). N=20, each data point averages 130 to 221 trials.

allocation (one-sample Wilcoxon test, $p = 3.81 \times 10^{-6}$, Figure 8B), indicating that participants have a bias towards distributing resources homogeneously among the selected alternatives. Lastly, we investigated whether such deviation from optimality affected the participants' reward (or outcome) in the task (Figure 8C). At each trial, the outcome is defined as the number of high-quality apricots among the 100 apricots purchased. We computed the differences between the observed and optimal outcomes (mean reward when following the ideal allocator) and observed a negative deviation

from optimality (mean \pm s.d.: -.56 \pm 1.30), which was only marginally significant ($t_{19} = -1.95$, p = .066). The lack of influence on the outcomes might be attributed to the prevalent use of low capacity (2, 3, or 4 samples) for which, even in the rich environment, the optimal sample allocation does not substantially differ from a homogeneous allocation. In conclusion, participants exhibit a significant bias towards homogeneously sampling alternatives, as previously found (Vidal et al., 2022), compared to what is predicted by the optimal allocator model (Moreno-Bote et al., 2020). However, this deviation had a minimal impact on their performance.

Discussion

Human behaviour is inherently variable, even when individuals engage in the same task over and over. For example, despite substantial practice and experience, professional basketball players will rarely reach free throw effectivity rates above 80%. Extensive research has explored the sources of this behavioural variability, often attributing it to stochastic neural processes (Faisal et al., 2008). Yet, recent evidence suggests that this variability should not be simply disregarded as noise (Garrett et al., 2013). Instead, it plays a significant role, notably in skill acquisition (Sternad, 2018) such as singing a new song (Ölveczky et al., 2005, 2011) or refining motor actions (Dhawale et al., 2017). Moreover, it fosters flexibility, facilitating exploration and the generation of novel behaviours, a particularly beneficial feature in uncertain environments (Kloosterman et al., 2019; Evans et al., 2019; Lee et al., 2023).

The present study delved into a less explored aspect of behaviour variability, focusing on the interplay between fluctuations in resource allocation and performance. We addressed whether behavioural variability during decision making is purely stochastic or else it is at least partially controlled, reflecting underlying strategies that go beyond the sole objective of maximising immediate reward. To investigate these questions, we employed a novel paradigm, the free Breadth-Depth dilemma (BD), which introduces a realistic scenario allowing for a better assessment of natural human decision-making. In this setting, individuals were tasked not only with determining which alternatives to explore in a block of consecutive choices but also the extent to which they explore them, granting them the freedom to strategise and plan fluctuations in resource allocation.

The BD dilemma involves active information sampling among multiple alternatives, in contrast to other paradigms that typically force binary choices (Daw et al., 2006; Weiss et al., 2021). Furthermore, BD dilemma diverges from the well-known exploration-exploitation dilemma (J. D. Cohen et al., 2007b), where information seeking can only occur at the expense of forgoing the currently rewarding alternative. Notably, in the BD dilemma, the allocation of search capacity must be made without immediate feedback—a situation mirroring one of the core features of planning, where decision outcomes are often available after a delay, and changes of mind come at a cost, as in when modifying previous reservations of accommodation or transport.

Summary of findings

Overall, this framework has proven to be relevant in uncovering and investigating fluctuations in capacity allocation. Indeed, when choice degrees of freedom is large in terms of variety of alternatives, and resource allocation can be freely distributed over alternatives and time, we observed significant deviations from an ideal allocator model. Most notably, participants distributed their initial capacity (N_c) non-uniformly among the choices, allocating sometimes less than the capacity ratio r of the block and sometimes more, resulting in fluctuations (trials with $C \neq r$, note that this definition includes skipped trials, where C=0). Crucially, the fluctuations observed in resource allocation cannot be simply attributed to passive stochastic processes. Indeed, these fluctuations were influenced by experimental manipulations, including available capacity (r) and choice horizon (N_{trials}), suggesting an active role and intentionality of the fluctuations. Moreover, these fluctuations demonstrated a discernible structure, indicating a 'savefor-later' strategy (Figure 6) and adaptation to recent reward history (Figure 7). We further characterised these fluctuations in resource allocation by extending the ideal allocator model (Figure 8). Indeed, while human search behaviour has often been deemed suboptimal within the narrow framework of reward maximisation (Beck et al., 2012; Wyart & Koechlin, 2016), behavioural variability may serve functional roles beyond this context (Renart & Machens, 2014). We identified strategies that individuals follow which add up to the policy maximising immediate return: entropy seeking, risk avoidance and the pursuit of information-gain, and further indicate the controllability behind their behavioural variability. Additionally, individuals exhibit diverse resource allocation across choices. influenced both by the available capacity within the block and by choice horizon (Figure 5). Despite these deviations from optimal, participants managed to consistently maintain a well-balanced breadth-depth trade-off, reflecting an optimal equilibrium between the amount of resources allocated and the number of alternatives considered (Figure 4). In this sense, the fluctuations in resource allocation do not stymie the rationality of the observed behaviour, confirming again their non-passive origin. Below, we discuss the implications of these findings.

Intentionality behind the fluctuations in resource allocation

The first crucial finding was that the fluctuations observed in resource allocation exhibit a discernible structure and should not be dismissed as mere noise. The results revealed that the occurrence of fluctuations varied depending on the experimental conditions. Participants were more inclined to skip sampling in a whole trial when search resources were scarce (low capacity), allowing them to garner larger amounts of information in other trials. The occurrence of skipped trials was also more pronounced when choice horizon was longer compared to shorter ones, suggesting a potential challenge in resource management (possibly reflecting Weber's law). However, on average, participants retained some capacity until the final trial in both short (mean±sd: 9.86±.34 out of 10) and long blocks (19.51±.97 out of 20), indicating effective capacity

management. The higher rate of skipping in longer blocks, rather than indicating an earlier resource exhaustion, might signify a more extensive exploration of diverse strategies, capitalising on the additional time to apply acquired knowledge (Carstensen et al., 1999; Wilson et al., 2014).

Secondly, two sequential effects were found regarding how participants allocated their resources in choices, further underlying that the fluctuations observed respond to a controlled strategy. Participants seem indeed to employ a 'save-for-later' strategy, allocating fewer resources (C < r) initially to conserve more resources for the subsequent choices (Figure 6). These findings underscore anticipation in participants' resource allocation strategy. While this approach does not guarantee the optimal immediate reward, it may exhibit some advantages especially when applied to real-world scenarios. This strategy serves as a secure means of managing finite resources (such as a monthly budget or the time allocated for an exam), preventing early depletion, and averting detrimental outcomes, such as financial overdraw or exam failure. Moreover, it could result in having more flexibility to adapt to unexpected changes in the environment or to explore new strategies in the future

In addition to being, at least partially, anticipated, evidence suggests that fluctuations in resource allocation also display flexibility by adjusting to recent reward history. Participants exhibit a greater likelihood of changing their strategy (shifting between sampling and skipping) following relatively lower outcomes (Figure 7A). What is more, the adaptive response to outcomes varies depending on the environmental context and seem to reflect violations in participants' expectations.

Individuals follow complex strategies beyond reward maximisation The observed structure underlying the fluctuations in resource allocation suggests that variability is, at least in part, a controlled process. By extending the optimal allocator model we further

identify three purposes behind those fluctuations which surpass immediate return maximisation and potentially offer valuable advantages in uncertain real-life scenarios.

Entropy seeking

First, our findings revealed that participants actively seek to explore various strategies by maximising entropy. In our task, entropy is maximised by allocated many different capacities C in trials of a same block. The pursuit of entropy maximisation holds significance for the acquisition of novel information and the generation of innovative behaviours, intentionally observed in animals as a means of escaping predators (Evans et al., 2019) or contributing to cognitive flexibility (Dajani & Uddin, 2015; Uddin, 2021). This adaptive behavioural strategy plays a crucial role in adjusting to uncertain environments and fostering creative thinking and problem-solving. As mentioned in the previous section, adaptive responses to outcomes could be linked to violations in participants' expectations. These two aspects, that is minimising surprises and maximising entropy, are pivotal ingredients of the free energy principle (Schwartenbeck et al., 2015). Such behavioural tendencies contribute to reducing predictions errors and establishing a more accurate model of the environment, facilitating rapid adaptation to potential changes. Moreover, the maximum occupancy principle, which favours entropy seeking, constitutes the core objective of newer theoretical frameworks modelling behaviour, offering an alternative perspective to reward maximisation (Ramírez-Ruiz et al., 2022).

Risk avoidance

Secondly, our observations indicate that participants adopt strategies that may reflect individual attitudes towards risk. Indeed, undersampling (allocating a capacity C < r) may have been employed to introduce fluctuations while mitigating the risk associated with skipping sampling and leaving some choices to chance (Figure S8). Research has demonstrated that individual differences in risk tolerance impact how limited resources are allocated, influencing performance (Tulloch et al., 2015). This bias affects the delicate

balance between the short-term risk of loss in outcome and the long-term benefits associated with learning. This underscores the necessity of incorporating individual features such as motivation (Zelick, 2007), curiosity traits (Risko et al., 2012), openness (Antinori et al., 2017) or beliefs associated with choice consequences (Loewenstein & Molnar, 2018) to enhance our understanding of the decision strategies humans adopt and why they deviate from a purely outcome-maximisation approach.

Information benefit

Lastly, our findings also revealed that in rich environments where obtaining high outcomes is frequent, participants adopt strategies aimed at maximising the probability of identifying a single bestsampled alternative (no tie), thereby facilitating the final choice. Previous literature has demonstrated that humans value information independently from reward (Gottlieb, 2012; Bromberg-Martin & Monosov, 2020) and engage in informative sampling by exploring the more uncertain option (Wu et al., 2018; Gershman, 2019; Schulz et al., 2019; Wilson et al., 2021). In our study, participants follow specific strategies that contribute to reducing uncertainty about the final choice. Conversely, this pattern does not hold in the poor environment, where most rewards obtained are low. It is conceivable that, in this scenario, participants place a greater emphasis on maximising immediate outcomes. In contrast, in the rich environment, where high rewards are easily attainable, the task may appear less challenging, allowing participants to seek more useful information

Close-to-optimal BD trade-offs despite fluctuations

Although individuals fluctuated in the number of resources they allocated within each choice (trial), they were consistent in the number of alternatives they sampled for a given allocated capacity. Indeed, our observations indicated that the BD trade-off remained unaffected by both the horizon (block length, Figure 4B) and the number of available resources (capacity ratio, Figure 4C), suggesting a robust stability in the way breadth and depth are

balanced. This underscores participants' capacity to minimise variability, once again suggesting a level of control over behavioural fluctuations.

Additionally, we successfully replicated two important findings regarding the allocation of resources among multiple alternatives (Vidal et al., 2022). First, our study revealed that participants follow a heuristic power-law sampling strategy, aligning with the optimal BD trade-offs (Moreno-Bote et al., 2020) and adapting effectively to the environmental richness (Figure 4A). Crucially, we did not observe any significant disparities between the optimal BD balance and participants' behaviour in both environments, as opposed to prior findings (Vidal et al., 2022). This difference might be attributed to the relatively lower capacity ranges employed in our study, which is conceivably easier to manipulate accurately. However, our paradigm also diverges by granting participants greater control over their information sampling, enabling them to choose not only what will be explored but also to what extent. Encouraging active engagement in a task, through methods like active learning, has been demonstrated to enhance performance significantly (Voss, 2010; Freeman 2014) and may have played a role here

Homogenous allocation within alternatives

Our study also replicated previous findings indicating that participants tend to distribute their capacity uniformly among the sampled alternatives (Figures 9 and <u>S9</u>). The origin of this bias is challenging to ascertain. It may arise from the increased ease of comparing fractions with a common denominator, thereby reducing cognitive load. Homogenous sampling could also emerge as a means to ensure that alternatives are equally risky, as they carry the same amount of information, aligning with humans' preference to standardise the uncertainty associated with the alternatives (Schulz et al., 2019; Wilson et al., 2021; Alméras et al., 2021). Finally, it may also stem from the visual presentation of the design and symmetry being aesthetically pleasing for humans (Attneave, 1955).

Further investigations are necessary to disentangle these potential causes, but the study already confirms the robustness of this effect.

Exploring the relationship between fluctuations and performance

Fluctuations resulting from future intentions or past rewards may contribute to reinforcing participants' sense of agency via the exertion of greater cognitive effort (Bussche et al., 2020), thereby influencing their task engagement and subsequent performance (van der Wel et al., 2012; Hon & Yeo, 2021). Notably, participants exhibiting increased fluctuations appear to adhere more closely to the optimal breadth-depth trade-off, particularly in the rich environment where an optimal balance may be more difficult to grasp as diverging from pure breadth (Figure S10). Although, our data is limited to properly assess the presence of this effect, this study could pave the way for investigating the impact of endogenous versus induced variability in resource allocation on participants' task engagement and on the adoption of strategies closer to optimality. Indeed, many studies exploring human information processing employ paradigms where participants lack control over information sampling (such as dot motion tasks: Glaze et al., 2015 ; sequences of stimuli: De Lange et al., 2010; Wyart et al., 2012; Cheadle et al., 2014)), which does not reflect the decision-making reality outside the laboratory. In real-world scenarios, individuals actively choose where to look at, what to listen to, or what to click on. Information acquired through one's actions, in contrast to passively received, has been shown to enhance performance (Ariely, 2000; Voss et al., 2011; Freeman et al., 2014), particularly through active hypothesis testing (Markant & Gureckis, 2014; Markant et al., 2016).

Limitations and further research

In summary, our findings highlight the utilisation of controlled strategies that, while diverging from optimality, exhibit features of anticipation and adaptation. These strategies require more cognitive effort than, for example, the homogeneous allocation of resources across choices. Actually, although effort is generally aversive (Kool et al., 2010; Kurzban, 2016), humans willingly engage in activities that demand increased effort, such as participating in charity runs, solving challenging sudoku puzzles, or assembling their own furniture (Inzlicht et al., 2018). Effort, therefore, is not solely balanced against the benefit associated with an action or computation (Kurzban et al., 2013) but can have intrinsic positive value and add to the perceived value of outcomes. Studies have shown that individuals are inclined to undertake more effortful actions when experiencing boredom. While we did not monitor participants' motivational or attentional states in our study, their interest in the task and their perception of its difficulty may have influenced their likelihood to pursue more complex explorative strategies (Milvavskava et al., 2021; R. Wu et al., 2023). For example, boredom has been identified as a factor promoting information-seeking behaviour (Geana & Daw, 2016; Danckert, 2019; Agrawal et al., 2022). Additionally, we did not observe a significantly higher number of skipped trials in the poor environment compared to the rich one, contrary to predictions from the optimal model. Indeed, although the proportions in which fluctuations exhibited by participants deviated from optimality significantly impacted their averaged reward, the loss in outcome was relatively small (Figure S4) and might not have been sufficient to incentivise a notable modulation in participants' sampling strategy. Manipulating the magnitude of rewards may be interesting to emphasise the gap between optimal and sub-optimal strategies (opportunity cost) and investigate whether humans are able to exert more effort to implement better sampling strategies and adapt their level of fluctuations.

Our study has other limitations associated with the assumptions of the ideal allocator model. Firstly, the model assumes that participants have complete knowledge of the posterior distribution of the success probability of the alternatives, which, in reality, they do not possess. Nevertheless, our findings indicate that participants can accurately infer the environment richness, as evidenced by their BD trade-offs aligning with optimality. Secondly, in terms of resource allocation across choices, our extended model performs well in predicting participant behaviour. However, the information benefit is estimated based on the optimal allocation of resources within a choice (how many alternatives are sampled – BD trade-off) and within each alternative (how many samples are in each alternative), and not on the observed allocations. While this assumption holds predominantly true in the poor environment, it is less accurate in the rich environment, especially for larger capacity allocations (C > 4). Notably, such trials are infrequent (8%), bolstering our confidence that this assumption does not undermine the robustness of our results.

Moreover, while our paradigm enables control over search capacity by manipulating the number of samples available, it does not incorporate the cost of sampling, a factor known to influence human and non-human primate sampling strategies (Petitet et al., 2021; Drugowitsch et al., 2012). In our experiment, all samples are standardized with the same cost (one coin = one sample), yet they may vary in computational costs, considering that allocating a sample to maximise potential information depends on the number and manner in which previous samples have been allocated. While the cost-benefit structure may have had a limited impact on our results due to the predominant allocation of low capacity, exploring the effect of fluctuations on performance (e.g., the BD trade-off) would necessitate accounting for the cost of sampling to comprehensively understand the goals and constraints underlying human search strategies.

Conclusions

To conclude, the results illustrate that human resource allocation behaviour is characterised by more variability than what the optimal model – maximising only immediate return – would anticipate, whilst still rendering a consistent near-optimal breadth-depth strategy. These findings shed light on the nature of behavioural fluctuations that help balancing the level of risk at stakes by enhancing information gathering, and the generation of diverse strategies whilst maintaining near-optimal performance. This may ultimately reflect advantageous and contextually relevant behaviours which imply anticipation, such as saving resources for later important choices, and flexible adaption based on past rewards and environmental conditions. Essentially, this work presents a novel framework that has proven useful to gain insights into the origins of behavioural fluctuations in the allocation of resources.

Methods

As the task is similar, methods describing the experimental design were adapted from Vidal and colleagues (2022). This study was pre-registered (https://osf.io/4dsma).

Experimental design

We developed a variation of the Breadth-Depth Apricot Task (Vidal et al., 2022) to test human search behaviour in sequential multiple economic choice scenarios under limited resources. The task was programmed using MATLAB (R2021b) and run using laptops with touch screens. Participants were initially introduced with a realistic narrative that provided a concrete everyday-life context to aid understanding the task goals and constraints. According to this narrative, at the end of each trial the participant purchases an order of apricots in bulk from one specific supplier, out of many available. The goal is to maximise the amount of good quality apricots accumulated throughout the experiment. Because suppliers vary in the proportion of good quality apricots they serve, participants are given the opportunity to sample suppliers' goods prior to the final bulk purchase, by spending some of their coins (capacity) in exchange for sample apricots. There are 20 available suppliers, but the total amount of available coins is limited so sampling all the suppliers is impossible. Based on the sampling outcomes in each trial, participants are to choose the supplier for the final purchase. In this study, we assigned fixed budgets for blocks of several consecutive purchases which can vary in length. Therefore, participants sample a limited number of suppliers at each trial or even choose not to sample any supplier before purchase (skipped trial) in order to save coins for future purchases or because the budget for that block is exhausted, in which case the supplier for the final purchase must be selected randomly.

Each trial (purchase) in the task was divided into a sampling phase and a final purchase phase, with participants having the possibility to skip this first phase (skipped trials). The number of coins spent during the sampling phase determines the search capacity of the participant on each trial. We manipulated the block length N_{trials} (10 or 20 trials) and the average number of coins available per choice in a block of trials (capacity ratio r: 2, 3 or 4), resulting in an initial capacity within a block N_c from 20 to 80 coins.

A video showing the proceedings of our experimental design is available <u>here</u>. On each trial, the remaining capacity (N_r) is clearly visible with the remaining coins being displayed, at any time, within the centre of the wheel (**Fig. 1A**). In each trial, the coins could be freely allocated one by one to any of the 20 suppliers by clicking the active coin in the middle of the display and then by clicking the desired supplier to sample from (**Fig. 1B.a**). Participants could arbitrarily allocate the coins in a given trial (i.e., all coins to just one supplier, or each coin to a different supplier, or anything in between). Once the desired number of samples has been allocated, participants doubled click on the sample in the centre to end the sampling phase (**Fig. 1B.b**). Only then the samples were revealed (**Fig. 1B.c**) as a binary outcome: either of good (orange) or bad quality (purple) apricots.

The sampling outcomes O_i at each supplier *i* (given the range 1 to 20) followed a binomial distribution $O_i \sim B(n_i, p_i)$ where n_i is the number of samples allocated in supplier *i* and p_i is the fraction of good quality apricots in that supplier. While n_i is chosen by the participants, p_i is unknown to them. Based on the information collected, participants could estimate p_i , and based on the estimation could choose amongst the sampled suppliers (and only the sampled ones) to perform a final bulk purchase of 100 apricots from a finally chosen supplier. We prevented participants from selecting a non-

sampled supplier to motivate a more careful search as, in case of only negative outcomes, one of the sampled suppliers would have to be selected anyway. The number of good quality apricots contained in the purchase was revealed (**Fig. 1B.d**), and the next trial (purchase cycle) started. The cumulative sum of good-quality apricots collected, as well as the number of trials and capacity remaining in the block, were displayed on the left of the screen throughout the experiment.

Independently in each trial and for each supplier *i*, the fraction p_i of good apricots was randomly drawn from a beta distribution (with parameters μ , ν). We considered two different environments, varying in the relative abundance of good apricots (p_i), denoted poor (μ =1/3, ν =1) and rich (μ =1, ν =1/3) (see the posterior distributions in Figure 3A). Participants were either presented to one or the other (but never to both) and they were verbally instructed about the relative richness of the environment they are in (poor / rich: "a majority of suppliers have a low / high proportion of good quality apricots"). Participants are aware that even though alternatives are different in each trial, they are extracted from the same environment. Providing participants with information about the prior distributions is pertinent, as the optimal model presupposes knowledge of the parameters α and β .

Participants were presented with 18 blocks (10 or 20 consecutive purchases with a fixed limited budget), composed of 3 repetitions of each experimental condition (capacity ratio and block length). Additionally, they were first presented with a practice block of 10 trials and a capacity ratio of 2 (these trials were excluded from the analyses). The whole experiment was self-paced, and opportunities were given to participants to rest after each block.

Participants

Participants were recruited through the CBC lab participants database (https://www.upf.edu/web/cbclab), with the criteria of being fluent in English or Spanish, with age between 18-55 and

being proficient with the manipulation of the touch screen as the task was performed on a touch screen laptop. Participants received a monetary compensation which was partly based on their final score at the task (number of good-quality apricots collected), ranging between a minimum of 9.30ε and a maximum of 10.60ε for an hour. Additionally, participants who obtained the three top scores in each environment condition (rich and poor), were rewarded with an additional 20, 10 and 5ε , respectively.

Participants were recruited until completing a valid final sample size of 20 participants in each of the two environment conditions (20 males, mean age \pm sd: 26.8 \pm 8.4 years). This initial sample size was decided in order to detect an effect of the environment on the BD trade-off with a 95% power (Cohen's d = 1.28, estimated from a previous study - see Vidal et al., 2022) and detect medium to large effect sizes with an 80 % power between and within participants respectively (more details in the preregistration: https://osf.io/4dsma).

Data from an additional 4 participants were discarded before analysis based on the pre-established criterion that they spent less than 90% of the initial block capacity (N_c) during the experiment. We considered that such behaviour could reflect participants lack of attention or understanding in the task. Another participant was discarded because of a technical problem which prevented him from completing the whole experiment.

Analyses

Analyses were run using R and MATLAB. Normality of the data was tested using Shapiro tests and homoscedasticity was tested using F tests or Bartlett tests (for more than 2 samples). In cases where it was possible, parametric tests were preferred, otherwise non-parametric tests were used. One sample Wilcoxon tests against the environment averaged outcome (25 and 75 respectively for the poor and rich environment) were used to test whether participant's final score was significantly higher than chance. For all participants, tests were significant (for $\alpha = .05$).

Sampling strategy

Our objective is to investigate how humans allocate limited search capacity over a series of choices to gather information about alternatives whose probability of success is unknown a priori. The sampling strategy covers three levels of behaviour. First, it is defined by how much capacity (number of samples, or coins) is allocated in each choice (trial). Second, it is characterised by how many alternatives are sampled (M) in a trial depending on the capacity spent (C). The relation between M and C defines the breadth-depth trade-off where a ratio M/C of 1 indicates a pure breadth, whereas lower ratios represent strategies leaning toward depth. Finally, the sampling strategy is also characterised by the way samples are allocated within each alternative. We first describe the allocation of resources within a trial, meaning the optimal breadth-depth trade-off and optimal resource allocation within the sampled alternatives (see also Moreno-Bote et al., 2020 and Vidal et al., 2022) and then introduce the optimal distribution of resources amongst the consecutive choices.

Optimal sampling strategy at the alternative level

The optimal sampling strategy is based on the work of Moreno-Bote and colleagues (2020), and we present the detailed information here. The framework assumes normative agents who do not exhibit any memory leakage and have knowledge of the environment priors (μ and ν). Specifically, normative agents aim to maximise expected reward and select the sampled alternatives that maximise the $\left(\sum_{i=1}^{s} O_{n,i} + \alpha\right)$

normative value $V_i = \frac{\left(\sum_{1}^{s} O_{s,i} + \alpha\right)}{N_i + \alpha + \beta}$, where $O_{s,i}$ represents the outcome of each sample s (1 or 0) allocated to alternative i drawn from the binomial distribution $B(n_{s,i}, p_i)$, N_i is the total number of allocated samples, and μ and ν are parameters that describe the beta distribution from which rewards in the environment are drawn. As the actual outcomes are unknown before the capacity is allocated, participants must compute the expectation of the maximum value of all sampled alternatives averaged over all possible outcomes given

environment parameters in order to determine the optimal allocation strategy.

The normative strategy is described at two levels, depending on the allocated resources (capacity C) and the richness of the environment. Firstly, at the trial level, it predicts the number of alternatives that should be sampled (Breadth-Depth trade-off, see Figure 2A). In a low-capacity scenario (e.g., C < 6 for a poor environment), the optimal allocator model predicts pure breadth, meaning that each resource sample should be allocated to a different alternative. As the capacity increases, a sudden change of strategy is observed, with the optimal number of sampled alternatives being approximately a power law function of the capacity (Moreno-Bote et al., 2020). Intuitively, when the agent has more resources, it is better to focus the samples on a few alternatives rather than spreading them across too many, as the latter approach would result in minimal discriminability between the quality of the sampled alternatives. The capacity at which the transition between pure breadth and the Breadth-Depth trade-off occurs depends directly on the richness of the environment. The poorer the environment, the later (at higher capacity) the transition will occur.

In the current experimental paradigm, participants determine the number of samples (capacity) to allocate in each trial. Consequently, at the individual level, we may have a limited number of trials or even none for certain capacities. To overcome this limitation and minimise potential noise, we chose to include in the analysis only capacities for which there were at least three observations (trials) from at least three participants when modelling the Breadth-Depth trade-off. This "rule of three" ensured a minimum level of precision in the measurements and was applied to all analyses and data visualisations, as required.

Secondly, the normative model predicts how many samples should be allocated to each of the sampled alternatives (Figure 2B). Indeed, for a given capacity C and number of alternatives sampled M, several resource allocations may coexist. For example, a capacity of four (C=4) allocated to two alternatives (M=2) may result in the allocation of 2 samples in two different alternatives each: $\{2,2\}$, or the allocation of 3 samples in the first alternative and 1 sample in the second: {3,1}. Visually, participants' resource allocation, in accordance with previous findings (Vidal et al., 2022), seems to favour homogeneous allocations of resources among the sampled alternatives (e.g., $\{2,2\}$) (Figure). However, particularly in deep allocations and rich environments, optimal behaviour involves nonhomogeneous allocations of samples to break ties (see Moreno-Bote et al., 2020 and Figures). To ascertain whether participants' allocations differ from the optimal ones, we used the same method as previously described by Vidal and colleagues (2022), consisting of computing the standard deviation of each sample allocation and comparing it to the standard deviation of the optimal allocation (predicted by Moreno-Bote et al., 2020) using a Wilcoxon test. We found significant deviations from optimality. To evaluate their potential effect on participants' performance in the task, we compared the observed outcomes (number of high-quality apricots purchased) with those obtained when following the ideal allocator strategy using a t-test. Since we were interested in deviations towards a more homogeneous sampling, we considered only trials where a pure breadth strategy is not optimal $(M_{opt} < C)$ (as in Vidal et al., 2022). However, in the poor environment, this condition is only satisfied when the allocated capacity is equal to or greater than seven, which corresponds to very few trials (166 in total). Therefore, we decided to focus our analysis on the rich environment, where we have sufficient data that satisfy this condition (3545 trials with $C \in [3, 10]$).

Optimal sampling strategy at the choice level

To establish how capacity should be optimally allocated amongst the choices (purchases or trials), we calculated the expected reward gain defined as the difference between the expected reward obtained during the purchase phase when sampling with a capacity C (using Monte-Carlo simulations and assuming an optimal allocation of samples within the alternatives – see section above) compared when selecting an alternative randomly (average prior distribution of the environment). We divided the reward gain by C to assess the unit reward gain per sample and infer the optimal behaviour. In the rich environment, we observe that the unit reward gain is maximised when sampling with a capacity of 2 and decreases with higher capacities (Figure 2C - right panel). In contrast, in the poor environment, the unit gain in reward is maximised for a capacity of 3 and is higher for a capacity of 4 and 5 compared to 2 (Figure 2C left panel). As a result, while in the rich environment, it is optimal to always allocate a capacity equal to the capacity ratio (Figure 2D - right panels), in the poor environment, fluctuations in the resource allocation are optimal for low-capacity ratio (r = 2) (Figure 2D – left panels). Indeed, it is therefore optimal to allocate 3 coins on a majority of times, or if not possible 4 or 5 samples per trial and to allocate zero capacity in the remaining trials (skip trials). Following this optimal allocation is associated with an averaged reward of 34.3 in blocks with 10 trials and 34.4 in blocks with 20 trials, while a homogenous allocation across choices is rewarded on average 33.0.

Model comparisons

Comparisons of Breadth-Depth trade-offs

As in Vidal and colleagues (2022), we explored individuals' sampling strategies by fitting the number of alternatives sampled M as a function of the capacity allocated C with three models, separately for each participant and block length experimental condition:

1. A piece-wise power-law model (*W*):

 $M(C) = \begin{cases} C^{a_1} \text{ if } C \leq B \\ C^{a_2} + b \text{ if } C > B \end{cases}, \text{ where } B \text{ corresponds to the breakpoint with } B \in \{3,4,5,\ldots,B_{max}\} \text{ with } B_{max} \text{ corresponding to the maximum capacity allocated minus one.} \end{cases}$

- 2. A linear model (*L*): M(C) = aC.
- 3. A power-law model (*P*): $M(C) = C^a$.

Linear and power-law models were compared using a paired Wilcoxon test on individual R-squared adjusted while power-law and piece-wise power law models were compared using ANOVA (with $\alpha = .05$) at the participant and block length levels. The power-law model captured the empirical relationship between *C* and *M* best in both environments.

Given the results of the model comparisons, the effect of the environment on participants' sampling strategies was therefore tested using the power-law model. We compared the power factor α extracted from power-law fits in each environment (rich and poor) using a Wilcoxon test, and in each block length (10 or 20 trials) using a permutation ANOVA with both block length and environment as factors. This analysis could not be used to compared BD trade-offs between capacity ratio conditions (r) as the range of capacities allocated differed greatly depending on r. Instead, we tested M depending on the capacity allocated, the ratio and the environment using a permutation test ANOVA.

Participants' BD trade-off were also compared to optimal (Moreno-Bote et al., 2020) by fitting the optimal values of alternatives sampled (M) depending on the capacity allocated for each participants (as participants used difference ranges of allocated capacity within trials), using the power law model (see Eq. 3). The power exponents obtained from fitting observed and optimal M were then compared with an appropriate test (t-test or Wilcoxon test) within each environment.

Fluctuations in the resource allocation

We considered variations in resource allocations (fluctuations), trials where the number of allocated resources differed from the capacity ratio of the block ($C \neq r$) (see Figure 4A). Among these variations, we identified three categories: trials with no capacity allocated (C=0), referred to as "skipped trials", trials with a non-null capacity allocated below the capacity ratio (0 < C < r), and trials with a capacity allocated above the capacity ratio (C > r).

As reported in the section above ('*Optimal sampling strategy at the choice level*'), the optimal observer predicts the occurrence of fluctuations only in the poor environment with the capacity ratio of two. To test these predictions, we first calculated the proportions of trials belonging to each category of fluctuations within each individual block, then averaged them across blocks, and finally averaged them across participants. We examined the impact of our factors of interest (ratio, block length, environment richness) on the occurrence of these fluctuations using linear mixed-effects models. Participants were included as random intercepts in the models.

For completeness we also described fluctuations in the resourcesallocation using two other methods. First, we computed the coefficients of variation (CV) of the sample allocation within each block, given by:

 $CV = std(\vec{P})/r$ with $\vec{P} = \{p_0, p_2, p_3, ..., p_{10}\}$ Where p_c represents the probability to allocate a capacity *c* inside a trial and *r* the capacity ratio of the block. Results are presented in the supplementary Figure S1 and reveal similar effects as when considering fluctuations as trials with an allocated capacity *C* different from the capacity ratio *r*.

Secondly, we computed the entropy H of participants capacity allocations within each block, given by:

$$H = -\sum_{c} p_{c} \cdot \log p_{c}$$

This measure does not control for the amount of resources available, but still reveal that fluctuations are larger in the longer compared to shorter blocks ($\chi_1^2 = 43.91$, $p = 3.44 \times 10^{-11}$). Results are reported in the supplementary Figure S2.

Extension of the ideal allocator model

We observed that participants exhibited more fluctuations in their resource allocations compared to what is optimal. To account for this phenomenon, we extended the optimal model to predict and explain the increased occurrence of these fluctuations. The variations in resource allocations allow for the sampling of certain trials with a higher frequency, enabling participants to gather more precise information about the quality of the alternatives. We proposed that one motivation behind these fluctuations is to ensure informative sampling, which means that sampling inform the selection of a better alternative (by avoiding ties for example). Another motivation could be to explore the amount of information and outcomes obtained by using different numbers of resources, contributing to a broader learning process of the environment. Additionally, we noticed substantial variability in participants' tendency not to allocate any resources in a trial (skipping). Randomly selecting a supplier for the final purchase may indeed be associated with increased risk and explain why some participants try to avoid such situations.

Consequently, we proposed a model where the expected utility (*EU*) to maximize is a weighted sum of different factors (Eq. 1). These factors include the expected reward R_c (following the optimal allocation of C samples), the information benefit I_c (weighted by a factor α), a penalty for skipping trials weighted by a factor β , and an entropy bonus weighted by a factor γ . The probability p_c represents the likelihood of using a capacity C in the block.

(Eq.1)
$$EU = \sum_{c=0}^{10} R_c p_c + \alpha \sum_{c=0}^{10} I_c p_c - \beta p_0 + \gamma \left(-\sum_{c=0}^{10} p_c \log p_c \right)$$

Here and below we don't write explicitly the dependence of EU and other variables on the parameters of the beta distribution μ and ν to simplify the notation.

For computational convenience, we considered capacities ranging from 0 to 10. Capacities exceeding 10 were excluded as their probability of occurrence in a trial is only 0.31%, and they are present in only 3.89% of the blocks.

Regarding the information benefit I_c , we modelled it in three different ways and estimated them using Monte-Carlo simulations (N=100 000).

(1) $I_{max, c} = E[max_i(S_{i,C}) | \mu, \nu, C]$

Where *i* runs over the alternatives sampled according to the optimal allocator, in a given environment, determined by the parameters μ and ν of the beta distribution, and with a given allocated capacity *C*.

We proposed that an informative sampling may be represented by the expected highest sampling probability $S_{i,C}$, with $\sum^{s} O$.

 $S_{i,C} = \frac{\sum_{i=1}^{s} O_{s,i}}{N_i}$. $O_{s,i}$ represents the outcome of each sample *s* (1)

or 0) allocated to alternative i and N_i is the total number of samples allocated to the alternative i.

This measure doesn't assume prior knowledge of the environments' prior distribution (μ, ν) . We hypothesised that such information benefit may be particularly valuable to guide the selection of a 'good' alternative in the poor environment where getting positive sample outcome $(O_{s,i})$ is very unlikely.

(2)
$$I_{single, C} = P(A_{\max(S_{i,C})} = 1 | \mu, \nu, C)$$

Where $A_{\max(S_{i,C})}$ stands for the number of alternatives with $S_{i,C} = max_i(S_{i,C})$.

The information benefit corresponds here to the probability of having a single alternative i with the highest sampling probability $S_{i,C}$. We hypothesised that, especially in the rich environment where receiving positive sampling outcome is very frequent, being able to distinguish the best sampled alternative (break ties) may drive participants sampling strategy.

(3)
$$I_{entropy, c} = -\sum_{c=0}^{10} p_{S_{i,c}} \log p_{S_{i,c}}$$

Finally, we proposed the information benefit to corresponds to Shannon's entropy (Rényi, 1961), as it is a common measure used to quantify information content. $p_{S_{i,c}}$ represents here the probability distribution of the sampling probabilities $S_{i,c}$ for a given alternative *i* and allocated capacity *C*.

We observe, in both environments, that the evolution of the information benefits as a function of the allocated capacity differs from the one observed in the expected outcome, suggesting its possible impact on participants' sampling strategy, independently of the reward (Figure S3).

An important limitation shared by all these information benefits is to be estimated based on an optimal allocation of samples within each capacity and environment. Results showed that participants closely follow optimal BD trade-offs in both environments (see Figure 3A) but within each alternative, the allocation of samples differs from the one maximising the reward, especially in the rich environment where participants have been shown to favour homogenous samples allocations (Figure 8).

We observed that in both the poor and rich environment, the model predicting the best the data was the one including $I_{single, C}$ (2) so we further reported models with $I_C = I_{single, C}$.

Model fitting

The underlying assumption of the fitting procedure consists in considering that the participants' behaviour arises from the optimisation of the expected utility EU given in Eq. 1. In other words, we assume that participants behave optimally with respect to a fixed set of parameters α , β and γ . Therefore, we first computed the optimal probabilities (that is, the one maximising EU) for a generic configuration of α , β and γ . p_c representing the probabilities of allocating a capacity C in a given trial within a block, they have to meet the following constraints:

1. $0 \le p_c \le 1$

- 2. $\Sigma_{c=0}^{10} p_c = 1$
- 3. $\sum_{c=0}^{10} p_c \cdot C = r$, where *r* represents the capacity ratio of the block.

This constrain entails that all the resources initially available in a block (N_c) are allocated. In the data, a significant number of blocks didn't comply with this constraint (135 blocks, 19.5%), however a great majority of them had only one sample not allocated (78 out 135). As a result, we chose to be more flexible and only excluded blocks for which less than the initial capacity minus one had been allocated (N_c -1; corresponding to 57 blocks, 8.23%).

To find the optimal probabilities p_c given these constraints we used the Lagrangian multiplier method. We looked then for the critical points of the following Lagrangian function:

(Eq.2)
$$\mathscr{L} = EU + \lambda_1 \left(\sum_c p_c - 1\right) + \lambda_2 \left(\sum_c p_c \cdot \mathbf{C} - r\right)$$

obtaining

(Eq.3)
$$p_c^* = e^{\frac{1}{\gamma} \left(R_c + \alpha I_c - \beta \delta_{0,c} + \lambda_1 + c \lambda_2 \right) - 1}$$

where δ_{0c} is the Kronecker delta and with λ_{12} given by imposing

(Eq.4)
$$\frac{\partial \mathscr{L}}{\partial \lambda_{1,2}} = 0$$

and

(Eq.5)
$$\frac{\partial \mathscr{L}}{\partial p_c} = 0$$

Note that the constraint (1) is automatically satisfied by the solution of Eq.3 and by satisfying the constraint (2).

A generic closed form solution for the Lagrange multipliers cannot be found (Abel-Ruffini theorem, not shown) and a numerical method is implemented to invert the equations for $\lambda_{1,2}$ (using the function *fsolve* in Python).

In such a way, the optimal probabilities can be computed per each α , β and γ . To fit these parameters, we minimised the sum S of the Euclidian distance between the observed probabilities p_c and the optimal predicted ones p_c^* and a penalty accounting for the size of α , β , γ , such as:

(Eq.6)
$$\mathbf{S} = \left| p_c - p_c^* \right| + \omega(|\alpha| + |\beta| + |\gamma|)$$

Where ω is a regularisation parameter. Different values of ω were tested to achieve a good balance between consistency of the parameters α , β , γ fitted and goodness of fit. As a result, a value of $\omega = 1$ was selected.

In order to compute criterions taking into account both the goodness of fits and the risk of overfitting (Akaike Information Criterion – AIC and Bayesian Information Criterion – BIC), we also computed the log-likelihood L of the data, given by:

(Eq.7)
$$\mathbf{L} = \log\left(\frac{N!}{\Pi_c n_c!} \Pi p_c^{*n_c}\right)$$

where n_c is the number of times a capacity c was allocated in the block, p_c^* the optimal probabilities extracted from the model and

(Eq.8)
$$N = \sum_{c} n_{c}$$

Model comparison is performed by comparing both AIC (Figure 7C) and BIC (Figure S7) as the latter favours more simpler models.

Sequential effects observed in the allocation of resources

• Intentionality in the sampling strategy

We delved deeper into the potential constraints and objectives associated with participants' behaviour in allocating little capacity (capacity C inferior to the capacity ratio r) in a trial, resulting in fluctuations in resource allocation. Specifically, we calculated the capacity allocated in a given trial based on its relative position to the nearest trials with C < r. This analysis aimed to investigate whether these trials are a product of anticipatory strategies or rather an adaptation after having previously over-allocated the available capacity.

• Sampling strategy and received outcomes

To explore the potential influence of received outcomes on participants' sampling strategy, we implemented a median split to divide the obtained rewards (number of good-quality apricots purchased) separately for sampled and skipped trials, considering that sampled trials typically yield higher rewards. Additionally, we categorised participants' sampling strategy into two groups: "sampling" (C>0) or "skipping" (C=0). Based on this categorisation, from one trial to the next, participants could either maintain the same strategy (sample-sample or skip-skip) or switch their strategy (sample-skip or skip-sample). Our investigation focused on how the magnitude of the outcome received in a given trial influenced the probability of repeating or, conversely, switching the strategy in the next trial. These analyses exclusively considered trials in which some capacity was still remaining ($N_r \neq 0$), ensuring that both behaviours (sampling or skipping) were feasible.

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Supplementary Figures

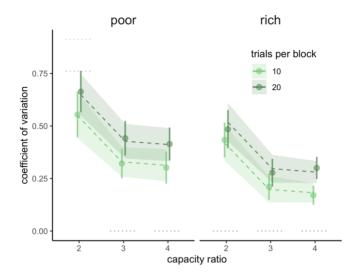


Figure S1. Participants capacity allocation fluctuates more when little capacity is available and with larger horizons. Coefficient of variation (CV) of the capacity allocated over the block depending on the capacity ratio *r*, block length (colours) and the environment (poor or rich). Vertical bars represent s.e.m. of the data, while dashed lines and shaded areas represent respectively the predicted averages and s.e.m. using LMEM. Dotted horizontal segments represent the CVs predicted by the optimal model. LMEM results reveal a significant effect of the ratio ($\chi_1^2 = 114.93$, $p < 2.2 \times 10^{-16}$) and block length ($\chi_1^2 = 23.71$, $p = 1.12 \times 10^{-6}$). No significant effects of the environment ($\chi_1^2 = 1.99$, p = .16), nor an interaction between the block length and the capacity ratio were found ($\chi_1^2 = .71$, p = .70). [back to Methods]

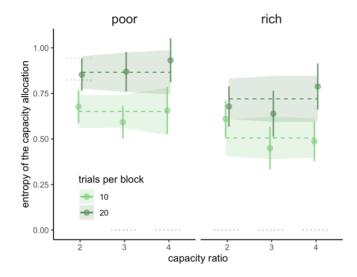


Figure S2. The entropy of participants capacity allocations does not significantly fluctuate depending on the experimental conditions. Entropy of the capacity allocated over the block depending on the capacity ratio *r*, block length (colours) and the environment (poor or rich). Vertical bars represent s.e.m. of the data, while dashed lines and shaded areas represent respectively the predicted averages and s.e.m. using LMEM. Dotted horizontal segments represent the CVs predicted by the optimal model. LMEM results reveal a significant effect of the block length only ($\chi_1^2 = 43.91$, $p = 3.44 \times 10^{-11}$). No significant effects of the environment ($\chi_1^2 = 1.35$, p = .25), the capacity ratio ($\chi_2^2 = 4.56$, p = .10), nor an interaction between the block length and the capacity ratio were found ($\chi_1^2 = 4.57$, p = .10). [back to Methods]

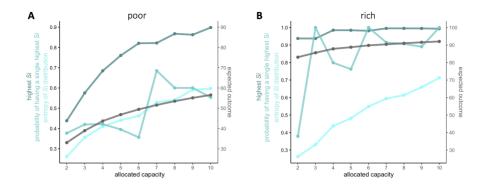


Figure S3. The information benefits evolve with capacity differently from the expected outcome. A-B. Mean highest sampled probability (S_i) of the sampled alternatives $(I_{max}, \text{darker sea green})$, mean probability that this highest sampled probability S_i correspond to a single sampled alternative and not several ones $(I_{single}, \text{medium sea green})$ and mean entropy of S_i distribution $(I_{entropy}, \text{lighter sea green})$. The mean expected outcome when selecting the sampled alternative with the highest normative outcome V_i is plotted in dark grey. The poor (A) and rich (B) environments are presented respectively in the left and right panels. [back to Methods]

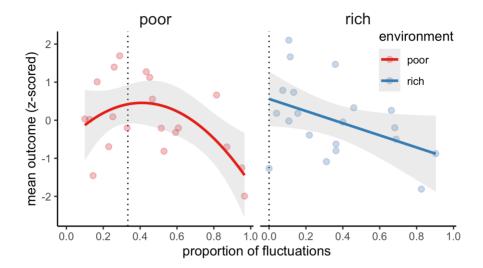


Figure S4. Participants outcomes are affected by their level of fluctuations in the resources allocation similarly as predicted by the optimal model. Participants mean outcomes received (z-scored by environment) depending on individuals' level of fluctuations, measured by the proportions of trials with the allocated capacity C different from the capacity ratio r. The vertical dotted lines correspond to the optimal proportions of fluctuations in each environment. The coloured lines represent the model best fitting the data (second-order polynomial or linear). [back to Results] [back to Discussion]

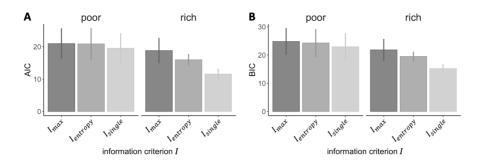


Figure S5. The information criterion maximising the probability to obtain a single best sampled alternative is predicting the participants search strategy the best. Averaged AIC (A) and BIC (B) across participants in the poor and rich environments estimated by fitting the data within each block using the full model (α , β and γ different from zero) with the. Three different information criterions (see Methods). [back to Results]

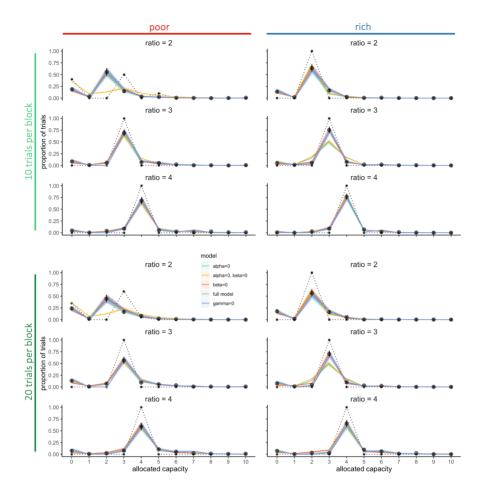


Figure S6. Resource allocations among choices are well predicted the extended optimal model (see Eq.1). Probabilities to allocate a capacity *C* from 0 to 10 depending on the environment richness (poor: left panels, rich: right panels) and the block length (10 trials per block: upper panels, 20 trials per block: lower panels). Black points represent the averaged observed probabilities across participants and vertical bars the s.e.m. Colours lines represent the averaged fitted probabilities for each model and the shaded areas the s.e.m. across participants and dashed black lines represent the optimal probabilities for each condition (model maximising only the expected reward). [back to Results]

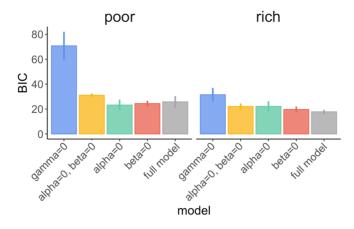


Figure S7. Averaged BIC across participants in the poor (left) and rich (right) environments estimated by fitting the data within each block using the five different models. [back to Methods]

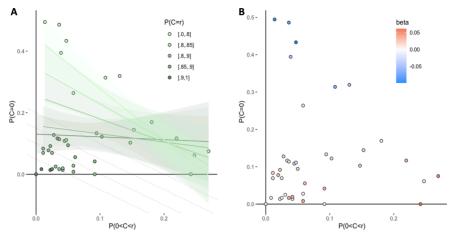


Figure S8. Participants whose resource allocations fluctuate follow a strategy which balances skipping sampling (C=0) and allocating little capacity (0 < C < r) depending on individual fitted risk aversion (β). A. Averaged individual probabilities to skip sampling depending on the probability to allocate a capacity inferior to the capacity ratio r. The colours represent the averaged individual probabilities to allocate a capacity equal to r (not fluctuating) and are also separated by the diagonal grev dotted lines. The coloured lines represent the correlation between both probabilities (skipping and allocating a capacity inferior to the ratio) including all participants (darker green) or participants with a minimum fluctuating probability (lighter greens). Shaded areas represent 95% CI. Results of these correlations are as follow: all participants: tau = .12, p = .28, N=40; participants with P(C=r) < .95: tau = -.01, p = .92, N=36; P(C=r) < .90; tau = -.24, p = .097,N=25; P(C=r) < .85: tau = -.46, p = .006, N=19; P(C=r) < .80: $\rho = -.86, p < 2 \times 10^{-16}$, N=16). B. Idem as panel A but dots are coloured depending on averaged individual estimated betas parameters of the best fitting model (full model in the rich environment and model with alpha=0 in the poor). Fitted beta parameters are found to decrease with the proportion of skipped trials (LMEM: t = -11.72, $p < 2 \times 10^{-16}$) and increase with the proportion of trials with an allocated capacity inferior to the ratio (0 < C < r) $(t = 5.93, p = 4.96 \times 10^{-9})$, revealing that participants with a large proportion of trials with 0<C<r are also characterised by a higher risk aversion (high betas). [back to Results] [back to Discussion]

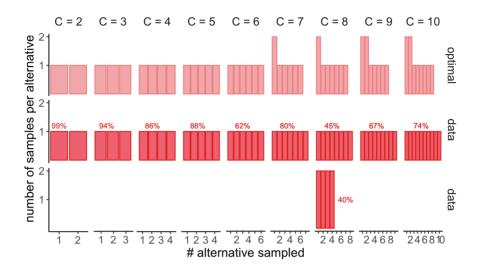


Figure S9. Participants have the tendency to homogeneously allocate capacity amongst the sampled alternatives. Number of samples allocated to each sampled alternative depending on the capacity allocated C in the poor environment. Upper panels: allocation of samples maximising the reward (optimal). Lower panels: most frequent allocations of samples observed across participants as a function of capacity. The allocations representing at least 50% of the trials are displayed and their likelihood is reported. [back to Results] [back to Discussion]

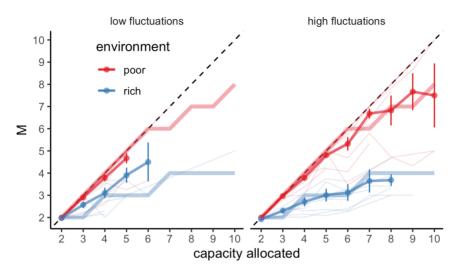


Figure S10. Fluctuating in the resource allocation seem to be associated with close-to-optimal BD trade-offs. Number of alternatives sampled (M) depending on the capacity allocated, the environment richness (colours) and the proportion of fluctuations (median split on individuals' proportions of trials with $C \neq r$). Group average and s.e.m. are plotted above individual data (thin light lines) and optimal values of M (thick light lines). Dashed lines indicate unit slope line. N=20 per environment. [back to Discussion]

5. GENERAL DISCUSSION

Maximising information is oftentimes the go-to strategy for achieving optimal choices, for example when deciding the route on a trip, buying a new phone, or resolving an exam question. Nonetheless, constraints such as limited time, financial resources, and cognitive capacity often hinder us from comprehensively processing all necessary information essential for making the best decisions consistently. This reality is particularly relevant in the present era. Contemporary society inundates us with a myriad of stimuli, meticulously crafted to capture attention and stoke desires, sometimes even tuned and targeted individually for us (Lorenz-Spreen et al., 2021), leading to an ever-growing list of perceived needs. Simultaneously, modern world propels us towards greater efficiency, not just in the professional environment but also in personal choices. This requirement demands that we seize lucrative sales offers while bearing in mind ethically mindful and environmentally friendly consumption. For instance, we are now presented with advertisements promoting reduced consumption ('desellers' or 'dévendeurs' - ARCOM) interspersed among commercials that encourage product purchases. As a result, the volume of information required for optimal decision-making is immense, and acquiring and processing this information incurs a cost that individuals may find challenging, both in terms of capacity and willingness to bear.

In this context, it seems relevant to understand how individuals confront demanding decision-making scenarios considering their inherent limitations, while striving to evade burnout or disillusionment. One may indeed be torn between contradictory information or feel insecure about past choices, fearing to have missed relevant information. While this thesis does not provide an exhaustive answer to this very broad question, we hope it provides useful insights. In particular, this research sheds light on three distinct experiments with specific choice scenarios, each one of them unravelling the strategies humans employ when confronted with complex choices that demand to strike a delicate balance between adaptability and efficiency.

5.1. Summary of findings

In our initial study, we explored how automatic behavioural tendencies, which are highly resource-efficient but lack flexibility, can be countered when they do not align with the current goal. We chose to focus on subjective value, known to be processed rapidly even when irrelevant for the task at hand and to influence both attention and decision-making. Using a binary choice task, we pitched subjective value (food preference) against an objective task goal (food price). We noted that preferred food items were indeed consistently chosen faster than less favoured ones, even without attentional or motor anticipation. However, the potentially negative

impact of subjective value on choice accuracy could be overridden by engaging stronger cognitive control, as evidenced by enhanced mid-frontal theta oscillations. Despite the reasonable inclination to prioritise value to seize favourable opportunities swiftly, it is crucial not to let potential rewards overshadow other relevant features necessary to achieve important goals. Our findings highlighted the role of cognitive control in flexibly disregarding subjective value when it conflicts with the current aim.

Moreover, we collected intracortical EEG data from a patient performing the identical task, aiming to identify the specific brain regions associated with the increased MFT power observed in scalp EEG (Appendix). Regrettably, our findings did not reveal oscillatory activity modulated by heightened engagement of cognitive control in the mid-cingulate cortex.

In our second study, we delved into the human ability to adapt search strategy according to the available finite resources and the richness of the environment. We focused on the Breadth-Depth dilemma, a choice scenario where individuals are confronted with an overwhelmingly high number of options beyond their capacity for thorough assessment, as it is often the case in real-life situations. Upon these situations, strategic decisions must be made on where to place the limited resources to extract information. By comparing participants' strategy to an ideal allocator model aiming to maximise rewards, we discovered that individuals adopt heuristics that adjust sampling to the environmental context, reaching a nearoptimal performance. This simplified strategy demonstrates flexibility and efficiency, reducing neural computation with minimal impact on performance.

In our third and last study, we aimed to better characterise spontaneous variability in human behaviour and how it relates to performance. Leveraging the fact that individuals adopt nearly optimal breadth-depth trade-offs, learned from the second study, we expanded the paradigm to investigate the allocation of finite resources over time. The behavioural fluctuations we observed were far from being mere random variability, and instead displayed a structured nature. We reasoned these fluctuations align with the pursuit of explorative strategies and pertinent information while mitigating risks. These nuances of behaviour indicate a multifaceted behavioural framework where immediate reward maximisation exists alongside other objectives that can be achieved through flexible control over the allocated search capacity.

In the reminder of this final chapter, I will outline the primary implications of the three studies presented in this thesis and discuss potential avenues for future research that they inspire. I will, however, try to avoid redundancy with previous chapters by not revisiting the conclusions already discussed individually on each chapter, which are briefly summarised above. Instead, I will put the focus of the discussion on reflections which have not been previously addressed in the earlier chapters, as well as those conclusions that transcend the individual studies.

5.2. Unveiling strategies to counter automatic behaviour

The inherent efficiency of automatic behaviours streamlines our responses to a variety of stimuli, so that our reactions are fast but relatively inflexible. Whether it's the attraction of attention sparked by loud noises, sudden moving objects, or the allure of high-reward choice alternatives (B. A. Anderson et al., 2011; Hickey et al., 2011; Libera & Chelazzi, 2006; Theeuwes & Belopolsky, 2012), these automatic responses often influence our decisions regarding other aspects of the stimuli, occasionally leading to biases (Summerfield & Koechlin, 2010; Blangero & Kelly, 2017; Corbett et al., 2023). The colour of a dot may be, for example, perceived more often as the colour associated with a higher reward, especially when responding fast (Afacan-Seref et al., 2018). The first chapter of this thesis delved into this intrinsic facet, particularly when an individual's subjective preference clashes with the current strategic goal. The study described therein proposed that individuals redirect their resources from highly desired but inadequate choices to less immediately desirable but convenient choices, by engaging cognitive control mechanisms, as indexed through behavioural variables as well as by mid-frontal theta (MFT) activity in the EEG.

These findings have revealed that subjective value associated with alternatives significantly biases participants' choices, irrespective of the choice's difficulty measured by the relevant goal-based evidence. This supports the existence of a fast and automatic boost of influence of subjective value on strategic decision-making, in the absence of any attentional or motor anticipation. Moreover, the study identified two distinct strategies that tend to mitigate this fast and automatic bias over time. One (expected) strategy involves signalling a conflict between value-based evidence and goalrelevant evidence and its regulation through the recruitment of heightened cognitive control. In another, unexpected strategy, some participants bypassed the increased need for cognitive control by relying on their prior beliefs about the features of the alternatives to inform their choices. In particular, participants who exhibited strong preference for expensive items were more prone to quickly select the items they liked the least, although least preferred items were not more often cheaper in the context of the task. Consequently, this pattern led to a heightened occurrence of errors in choices when the preferred item happened to be the cheapest, thus reversing the expected congruence effect.

In line with this explanation, the study presented in the first chapter found a correlation between the strength of prior beliefs regarding the relation between the items' price and preference, and the participants' tendency to avoid engaging additional cognitive control when faced with evidence contradicting subjective preference. Indeed, attesting that many times the correct alternatives do not align with their prior beliefs may require to update their perception of the world which is costly and has a negative impact on confidence. This reliance on prior beliefs, which we have measured here using foodstuffs, resonates with findings in the realm of political opinions. This research indicates that individuals with more extreme or entrenched political views exhibit less inclination to alter their perspectives (cognitive inflexibility – Zmigrod et al., 2019) or to seek information that challenges their initial opinions (Brandt et al., 2015; Ditto et al., 2019). Understanding how to motivate individuals to invest effort in considering information conflicting with their viewpoints is pivotal across various contexts.

One compelling aspect that has piqued my curiosity from the findings of the first study involves the decoupling between value biases observed on choice accuracy and those observed on response time. Traditional conflict tasks (M. Botvinick et al., 2004; Cavanagh & Frank, 2014) or value-biased choices (Summerfield & Koechlin, 2010; Noorbaloochi et al., 2015; Afacan-Seref et al., 2018; Corbett et al., 2023) typically show a consistent reduction in accuracy and slower response times in incongruent choices when there is a mismatch between the goal-relevant information and irrelevant conflicting evidence (such as the colour of the words in a Stroop task or asymmetric reward in a binary choice). However, in our first

study, congruency is defined by the relation between an item's estimated price and participants' pre-existing subjective preference. In this context, choices tend to exhibit biases either favouring individuals' preferences or contradicting them, particularly in cases of robust prior knowledge about item value-price characteristics. In the meantime, the influence of value on reaction times is very consistent, with faster responses when participants opt for their preferred alternative across the board.

Moreover, an interesting observation emerged from this disparity between value bias affecting choice accuracy and response time: although the latter remains constant throughout the task, individuals with strong prior beliefs exhibit time-sensitive effects on both choice accuracy influenced by value and mid-frontal theta (MFT) enhancement in response to value-price conflict. Consequently, this temporal influence results in a higher frequency of selections of the least preferred alternative. This decoupling implies that the slowdown in responses in favour of the non-preferred alternative cannot be solely attributed to the increased engagement of cognitive control mechanisms, as measured by MFT oscillations. This discovery uncovers a complex experimental framework where automatic processing of evidence, such as subjective value, and expectations regarding features of the environment concurrently influence decision-making processes. It also offers an opportunity to delve deeper into understanding the stage of decision formation these signals have an impact on, and the intricate relationship they share with the engagement of more cognitive control resources.

5.3.Optimal allocation of limited resources; moving towards more complex scenarios

The exploration addressed in the second chapter of this thesis revolved around how individuals grapple with the challenge of decision-making when confronted with an overwhelming number of alternatives that surpass their capacity for comprehensive assessment. In these contexts, not uncommon in our everyday life, the question is: how many alternatives does the decision maker sample, and how deeply? To understand this resource-allocation problem we introduced the Breadth-Depth (BD) dilemma and developed the 'Apricot purchasing task', which marked a significant leap forward in comprehending how individuals manage limited search capacity. Through Studies 2 and 3, we revealed that humans gravitate towards assessing the statistically optimal number of alternatives. They adopt heuristics that minimally impact performance (as compared to the optimal decision maker) while displaying an impressive ability to flexibly adapt to available resources and environmental context, integrating the probable success rate of these alternatives (Vidal et al., 2022).

Despite the characterisation of the BD dilemma presented in Chapter 2 which introduces a much more complex decision-making

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problem than it is usually presented in the literature, it is clear that exploring increasingly complex scenarios in future research could shed additional light on decision-making processes. For example, real-life scenarios seldom present entirely novel environments. Instead, the options available often stem from previously known or present readily available information, sometimes strategically designed to kindle curiosity and desire (visually pleasant or intriguing images, brand logos, etc). In such contexts, can individuals still effectively disregard a large proportion of alternatives to focus on a subset in a statistically near-optimal fashion? Are they instead going to be overwhelmed by the sheer volume of information and choices at hand, or worse be systematically led further off the statistically optimal regime?

In the introduction I drew the distinction between the exploration-exploitation and the current BD dilemmas. However, extending the BD dilemma to encompass scenarios without delayed feedback would offer insights into situations where both breadth-depth and exploration-exploitation dilemmas intersect. For instance, consider the act of purchasing products in a supermarket. Initially, one might have a look at multiple products quickly, gradually narrowing down options as they gather information. The BD trade-off dynamically evolves over time, contingent upon the resources one is willing to invest before finalising a purchase and the desired level of confidence in their decision. Understanding optimal behaviours in such situations holds immense real-life relevance,

particularly in visual search contexts where the sampled information is immediately accessible.

5.4. Endogenous variability in the pursuit of individual goals

The third study of this thesis has been centred on the intricate variability inherent in human behaviour, aiming to illuminate the nuanced interplay between immediate reward focused strategies and approaches serving additional, longer-term objectives. By extending the BD Apricot task introduced in Chapter 2 to the management of limited search capacity for many alternatives across consecutive choices, we observed that participants demonstrate anticipation and adaptability in the way resources are managed over time. These fluctuations reflect an internally driven variability that unfolds across choices, each independent yet collectively strategic.

Despite being sub-optimal if we consider solely immediate reward maximisation, the behavioural fluctuations detected in the third study were not just noise. Rather, they seem to underscore the exploration of diverse strategies, risk minimisation concerning leaving certain choices to chance, and the quest for pertinent information crucial for informed decision-making. While these behaviours are suboptimal within the limited context of our experimental protocol, they exhibit strong potential benefits in uncertain and dynamic real-life environments. Indeed, exploring multiple strategies may be, in the long run, highly beneficial in case of changes in the environment or of the goal itself. Additionally, making informed choices is crucial not only when deciding but also afterward, enabling self-justification and confidence in one's choices, which holds particular importance in environments like the workplace.

Furthermore, I believe that this variability in behaviour may both adapt to and reflect individuals' personalities and their level of engagement in a task. For instance, the likelihood of exploring new strategies for information sampling may indeed hinge on individuals' motivation (Cerasoli et al., 2014; Zelick, 2007) and on individual traits related to curiosity (Risko et al., 2012). Specific curiosity traits have been linked to varying use of limited external resources such as money, energy, and time (Kashdan et al., 2018). Additionally, individual attitudes toward risk-taking may influence their inclination to explore and acquire novel experiences (Zuckerman, 1994), and may be impacted by the perceived cognitive load of the task (Deck & Jahedi, 2015). Gaining insights from these specific features could be relevant for a deeper understanding of individual differences that propel the pursuit of particular goals and for a more accurate characterization of inherent variability in information search strategies.

5.5. Humans: more than cognitive misers?

Humans have been labelled as "cognitive misers" (G. Allport, 1954) due to their inclination to evade unnecessary mental exertion (Kool et al., 2010; Taylor, 1981). Indeed, it is relatively easy to recall instances where we have acted as devotees to the minimum effort principle. Without contradicting this doctrine, the triad of studies showcased in this thesis generally delineates scenarios wherein individuals opt for simplified, lower cost strategies compared to the optimal ones. They adeptly navigate decision-making by employing heuristics in the way search capacity is allocated across alternatives (e.g., power-law BD trade-offs, homogeneous allocation), or relying on entrenched prior beliefs. Yet, these studies have also revealed the human capacity to employ more complex multifaceted strategies that transcend mere immediate reward maximisation objectives and flexibly adapt to potential opportunity costs associated with a choice.

These instances, where individuals pursue intricate strategies involving multiple goals, potential losses, or anticipation, exemplify how individuals can both under and overexert cognitive resources when tackling a problem. This begs the question: are humans truly cognitive misers? Or more precisely, when do people choose to spend cognitive resources and to what extent? The allotment of cognitive resources appears contingent on a delicate equilibrium between perceived benefits and losses, which can be influence by many intrinsic features such as fatigue levels or motivation but also by the availability of alternate strategies, such as reliance on prior knowledge, which, while less effortful, might be marginally less efficient. This question holds immense significance when seeking to evaluate human optimal behaviour within specific circumstances.

It's crucial to acknowledge that the majority of scenarios replicated within laboratory settings are highly artificial and may lack real-world relevance. Our brains, however, are specialized to function in high-dimensional uncertain environments encountered previously or plausibly encountered in the future. Therefore, an inability to optimally navigate artificial situations prevents extrapolation regarding the humans decision-making strategies (Nastase, 2020) and the limits of brain performance. Based on this, and although there is still a large margin of improvement, this thesis had the objective to tackle this problem by employing more realistic stimuli and immersing participants in more multifaceted and meaningful scenarios to better understand the intricacies of human behaviour. This approach may also help to accelerate the learning of the task and limit its potential influence on our conclusions regarding human competence and rationality (Lejarraga & Hertwig, 2021).

Moreover, the use of ecologically valid paradigms necessitates providing participants with sufficient incentives (Barbosa et al., 2022), mirroring those naturally present in real-life situations. Human subjects, even if capable of optimal performance in experimental tasks, might choose not to allocate adequate resources. Consequently, incentivizing participants involves appropriately calibrating task difficulty to stimulate engagement while preventing boredom and fatigue that could precipitate unexpected errors.

By scrutinizing behaviour through paradigms boasting stronger ecological validity, we inch closer to comprehending how humans manage their limited cognitive and external capacity when making decisions. Moreover, this approach may inform the design of environments where individuals willingly invest resources in the pursuit of more meaningful and indispensable goals. However, by charting further into this relatively unknown territory, we have run the risk of falling into some pitfalls, some of which I briefly discuss below.

5.6.Limitations

The inclusion of more ecological paradigms in research presents a substantial advantage in capturing the intricate nature of naturalistic human behaviour. However, their inherent allowance for increased participant freedom and decreased control introduces challenges in disentangling the many hypotheses often underlying unexpected observations. This trade-off between internal and ecological validity is a well-known problem when extrapolating research principles (Soto-Faraco et al., 2019; Matusz et al., 2019) and is a common limitation evident across the three studies presented in this thesis.

In the initial study, we observed that subjects employed diverse price-minimisation strategies - one seemingly reliant on cognitive control and the other on prior beliefs - generating mixed results concerning the impact of subjective value on choice accuracy. In the third study, we highlighted that participants' sampling strategies in rich environments, abundant with highreward alternatives, aimed not only to maximise rewards but also to access pertinent information for guiding their final decision. Upon reflection, such a goal might have influenced the results of the second study, where no discernible difference in Breadth-Depth (BD) trade-offs was found between rich and neutral environments. This balance was primarily tilted toward depth in the neutral setting. In neutral environments where the majority of alternatives are of averaged quality (gaussian distribution), participants tended to sample deeper than predicted by the optimal allocator model, potentially increasing the likelihood of obtaining valuable evidence for informed choices. Furthermore, while explicitly observing that participants adopt strategies aligned with multiple objectives in the third study, exploring the specific or in contrary general conditions in which these goals prevail remains a challenge. Assessing participants' perceived difficulty and engagement in the task could help grasp these issues. However, limitations persist concerning the

comprehensive examination of the diverse motivations driving human behaviour.

In a broader context, although modelling and exploratory analyses of results aided in characterising the use of various strategies, our capacity to discern the origin of the individual differences observed remained limited. Introducing metacognition measures to better define participants' experiences could have yielded useful insights in why some individuals preferred simpler strategies while others engaged in more complex approaches. Evaluating aspects such as participants' motivation in the task and confidence in their choices could help assessing their inclination to actively optimise their behaviour (Shenhav et al., 2013; Boureau et al., 2015).

5.7.Conclusions

This thesis has been dedicated to enhancing our comprehension of how individuals navigate the challenges and limitations inherent in decision-making involving complex scenarios. It specifically focuses on the disproportion between the vast array of choices and information present and our capacity to assimilate and evaluate the necessary evidence to make optimal choices within an allotted time or capacity. Our findings underscore the remarkable efficiency with which humans deploy adaptable strategies, considering available resources, environmental contexts, and the potential reliance on automatic behaviours, prior knowledge, and heuristic approaches. These strategies, despite their minimal impact on overall performance, appear to demand much less cognitive effort than fully optimal behaviours. It is noteworthy that individuals often settle for satisfactory choices rather than continuously striving for the ideal. Similar to the idea of decreasing marginal returns in economics, it would seem that humans 'stop investing' when an additional unit of mental resources renders too little increase in outcome. This notion should be pivotal when assessing for the optimality of human behaviour.

A crucial aspect lies in better understanding what exactly defines optimality for humans, unravelling the driving forces behind our behaviours to delineating where our attention should centre. This research unveiled diverse decision-making strategies, which may not necessarily indicate poor performance but rather the pursuit of individual, specific objectives and the utilisation of simpler strategies that may not be universally accessible.

Furthermore, optimality hinges on balancing expected rewards against the efforts required to attain them, in addition to integrating current goals and anticipating future needs. Employing innovative experimental designs that simulate real-life scenarios, incorporating naturalistic stimuli, numerous alternatives, and active information search, this study lays the groundwork for comprehending the intricate elements influencing human decision-making in complex environments.

As it often happens in scientific exploration, this thesis likely raises more questions than it resolves. Nevertheless, within this quest for understanding, our limited resources serve as a means to acquire knowledge that remains inherently, and fortunately, boundless.

Appendix: COGNITIVE CONTROL OR CONTROLS?

An attempt to localise the sources of mid-frontal theta increase related to context-specific cognitive control with intracortical EEG recordings.

Abstract

In our previous study, we observed that mid-frontal theta oscillations (MFT) correlate with indicating the necessity for heightened cognitive control, specifically linked to monitoring conflict, errors, and anticipated loss. To localise the neural network(s) associated with these diverse signals, we collected behavioural and intracortical (iEEG) data from a single participant performing the identical price minimisation task. As anticipated, behavioural outcomes demonstrated that swift responses favoured preferred items, consistently leading to quicker selection of preferred items. Analysis of iEEG recordings revealed heightened gamma activity in frontal areas (midcingulate cortex and precentral regions), but we did not identify any region specifically responsive to increased cognitive demands.

Introduction

Enhancements in mid-frontal theta oscillations and BOLD activity in the anterior/middle cingulate cortex (ACC/MCC) and associated prefrontal regions (especially the dorsolateral prefontal cortex; dlPFC) have been linked to diverse cognitive processes, notably conflict, error monitoring and expected rewards or losses (Carter et al., 1998; MacDonald et al., 2000; Botvinick et al., 2001; Ridderinkhof et al., 2004). The presence of these similar activation patterns across varied contexts has fostered a unified perspective, suggesting their role in signalling the need for cognitive control which facilitates both within-trial (slower response times, improved accuracy) and between-trial adjustments (post-error slowing, Gratton effect). In chapter I we presented a study where mid-frontal theta activity (MFT) increase was indeed observed in EEG in multiple cases: preference-price incongruence, following incorrect responses and in relation to the expected loss associated with the choice (ΔP). While all these situations lead to the idea that MFT is a general marker signalling the need for cognitive control, we were interested to identify the underlying neural network at play and wondered whether it was the same generating those context-specific MFT activities.

Indeed, several studies that directly compare cognitive control signalling in response to conflict or errors propose a functional dissociation between MFT and BOLD activity in terms of frequency, localisation, strength, and duration (Ullsperger & Von Cramon, 2001; Nee et al., 2011; Cohen & Van Gaal, 2014; Iannaccone et al., 2015; Muralidharan et al., 2023). A key distinction primarily lies in the peak theta frequency: conflict-related theta typically resides within the high theta range (6-8Hz), whereas error-related theta predominantly falls within the low theta band (4-5Hz). This distinction was replicated in our first study (see Figure 1).

Furthermore, conflict-related theta is not phase-locked to stimulus onset or the response(Nigbur et al., 2012; Cohen & Donner, 2013), unlike error-related theta, which is partly phase-locked to the response and associated with the error-related negativity (ERN) evoked potential(Luu et al., 2004; Cavanagh et al., 2009; Cavanagh & Frank, 2014). A recent investigation employing simultaneous EEG and fMRI recordings (Beldzik et al., 2022) further explores this distinction. Using classic conflict paradigms (Stroop and Simon tasks), similar MFT power enhancement (4-8Hz) in response to conflict and following errors were found in EEG. However, a negative correlation between conflict-related theta and dmPFC BOLD activity was found, while error-related theta exhibited a positive correlation with the activity in the MCC. These findings raise challenges in translating signals observed in EEG to those in fMRI and question the role of the cingulate cortex in generating MFT oscillations during conflict. Additional studies substantiate these uncertainties, revealing various sources of midfrontal theta (Töllner et al., 2017; Zuure et al., 2020), linked to conflict-related processes but also independent from conflict (Mückschel et al., 2017; Töllner et al., 2017).

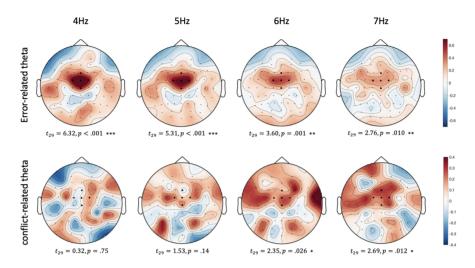


Figure 1. Error-related theta seems prominent at lower theta (4-5Hz) while conflict-related theta is solely present at high theta (6-7Hz). Topographic maps of power analyses (4 to 7Hz) contrasted between incorrect and correct trials (error-related theta) from the 500ms time window post-response (upper panels) or between incongruent and congruent correct trials (conflict-related theta) from the -450 to 50ms time window relative to response (lower panels). Power analyses are baselined with the 500ms window pre-stimulus onset. Results of paired t-tests testing the averaged power extracted from mid-central electrodes (larger black dots: Fz, FC1, FCz, FC2, Cz) between conditions (incorrect vs. correct, incongruent vs. congruent) are displayed below each map. N=40.

In an attempt to elucidate these inconsistent findings, we had the opportunity to collaborate with Hospital Clinic in Barcelona to conduct our price minimisation task (see Methods in Chapter I) in patients with drug-resistant epilepsy undergoing intracranial EEG (iEEG) monitoring. Regrettably, our data collection was limited to just one participant, for which monitoring of prefrontal as well as midcingulate areas was planned. Nevertheless, we deemed it valuable to present these findings and engage in further discussion regarding the utilisation of iEEG recordings to precisely delineate the brain network(s) signalling distinct cognitive control requirements.

Methods

Ethics statement

The study was conducted in accordance with the Declaration of Helsinki and informed consent was explicitly obtained from all participants prior to the recordings and the performance of the tasks. All diagnostic, surgical and experimental procedures have been previously approved by The Clinical Ethical Committee of Hospital Clínic (Barcelona, Spain). In particular, the specific proposal to run the cognitive experiments for this study was approved in March 2020 under the code number HCB/2020/0182.

Participant

Intracranial EEG recordings were acquired during performance of the price minimisation task (see Chapter I – Methods) in one subject (male, 32 yo) with pharmacoresistant epilepsy during the diagnostic monitoring period in Hospital Clínic (Barcelona, Spain). The participant had normal vision.

Behavioural task

The participant performed the exact same task as the one described in the previous chapter of this thesis (price minimisation task). The participant met the inclusion criteria outlined in the Methods section of Chapter I (*'Experimental Conditions'*). We applied the identical rejection criteria on the trials as used in Chapter I and pre-registered (https://osf.io/msdzx). In total 1001 trials were included in the analyses (C_0 : 303, C_+ : 333, C_- : 365).

Data acquisition

LFPs were recorded using 13 intracerebral multiple contact Microdeep® platinum–iridium Depth Electrodes (Dixi Medical, Besançon, France; diameter: 0.8 mm; 5–18 contacts, contact length: 2 mm, distance between contacts: 1.5 mm) that were stereotactically implanted using frameless stereotaxy, neuronavigation assisted, and intraoperative CT-guided O-Arm and the Vertek articulated passive arm. In total, 151 contacts were implanted and recorded (see Table 1 for details and Figure 2 for post-implantations schemes). The decision to implant, the selection of the electrode targets and the implantation duration were entirely made on clinical grounds using the standard procedure (Cardinale et al., 2013; Lachaux et al., 2003). All recordings were obtained using a standard clinical EEG system (XLTEK, subsidiary of Natus Medical) with a 2048 Hz sampling rate. All signals were referenced to the scalp electrode CPz. A pre-implant Magnetic Resonance Imaging (MRI) T1 scan and a post-implant computed tomography (CT) scan were used to determine contact localizations. MR scans were obtained with a 1.5 T unit (Magnetom Aera 1.5 T; Siemens Medical Systems, Erlangen, Germany) with a specific protocol that included the following sequence: sagittal T1-weighted gradient recalled (repetition time [TR] 20 ms, echo time [TE] 7.38 ms, Flip Angle [FA] 20, 1 mm slice thickness).

Anatomical localisation of the SEEG electrode contacts and definition of regions of interest

Contact anatomical locations were identified from the individual subject's pre-implant MRI after coregistration with the post-implant CT scan. The CT was co-registered to the T1 and contact tags and names were placed manually using fieldtrip's toolbox (https:// www.fieldtriptoolbox.org/). Scans were then analysed by visual inspection using Brainstorm (v3). Selection of channels was done in native space to prevent errors. First, contacts were labelled either as grey matter (GM) or white matter (WM). Electrode contacts span a volume 2 mm long with a radius of 0.4 mm. Previous research suggests that electrical fields generated in GM can be measured by contacts in nearby WM up to $\approx 1/1.5$ mm away (Buzsáki & Wang, 2012; Arnulfo et al., 2015; Narizzano et al., 2017) or even further when analysing low frequencies using a monopolar referencing scheme (Vila-Vidal et al., 2023). Based on this assumption, WM contacts lying at a distance up to 1 mm from GM regions with no contact inside were assigned to that region and classified as GM. Contacts lying outside brain tissue or within altered brain tissue according to clinicians (e.g., heterotopias, focal cortical dysplasias) were excluded from the analysis. The electrode contacts lying in the suspected epileptic focus were identified by clinical experts using gold-standard procedures and were also excluded from the study.

The contacts of interest for this study were defined as those lying in the frontal lobe or in the anterior half of the cingulate cortex. ROIs (regions of interest) were defined as usually expressed in the cognitive literature based on fMRI and electrophysiological studies (e.g. dlPFC, vlPFC, M1, PMC). For the purpose of this study, the dlPFC (dorsolateral prefrontal cortex) was defined roughly as the middle frontal gyrus, the vIPFC (ventrolateral prefrontal cortex) was defined as the inferior frontal gyrus and the superior parts of the pars triangularis, pars orbitalis and pars opercularis. M1 (primary motor cortex) was defined as the precentral gyrus and PMC (premotor cortex) was roughly defined as corresponding to Brodmann area 6, that is, as a vertical strip extending from the cingulate sulcus to the lateral sulcus, including caudal portions of the superior frontal and middle frontal gyri, and rostrally bounded by the precentral gyrus. The supplementary motor area (SMA) was located in the medial region of the frontal lobe, superior to the cingulate sulcus in Brodmann area 6. The midcingulate cortex (MCC) is defined as the caudal and posterior part of the Brodmann area 24 (area 24') situated above the corpus callosum. Table 1 summarises the number of contacts and electrodes of interest and their locations in the cortex. According to the initial planning the electrode FAIL (which stands for "frontal anterior inferior left" was supposed to enter the patient's brain through the dlPFC. Upon inspection of the post-implant MRI, its superficial contacts were found to be located in the precentral gyrus, more posteriorly than initially planned. Activity recorded from these contacts is, nonetheless included in this study, in order to illustrate the extension of our analysis paradigm with iEEG.

Electrode	Contact numbers	Functional area		
FAS	1, 2, 4, 5	SMA		
FAIL	9, 10, 12, 13, 14	Precentral gyrus		
FAIL	1	MCC		

Table 1. Regions of interest (ROI) monitored in the patient localised in the frontal lobe and expressed in terms of the functional areas. For each electrode, lower contact numbers represent deeper positions in the brain. SMA: supplementary motor area, MCC: midcingulate cortex.

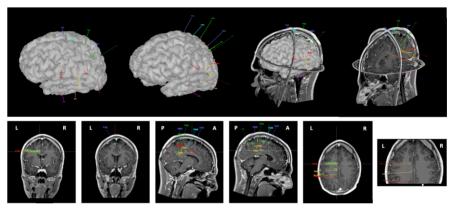


Figure 2. Participant post-implant MRI brain scans showing different electrode trajectories in sagittal, coronal and horizontal planes (bottom) and 3D brain reconstruction (top). The electrodes of interest (FAIL and FAS) are presented in red and purple, respectively.

iEEG signal pre-processing

Besides the contacts mentioned in the previous section, we also excluded from the computational analysis contacts displaying highly non-physiological activity. SEEG signals were preprocessed using custommade code in Python 3 based on the Numpy, Scipy, and MNE libraries. Signals were analysed in the monopolar montage (reference to CPz). Prior to the main analysis, signals were low-pass filtered with a zero-phase FIR filter with stopband at 900 Hz to remove aliasing effects. A high-pass zero-phase FIR filter with stopband at 0.1 Hz was also applied to remove slow drifts from the SEEG signals. Additionally, we also used a band-stop FIR filter at 50 Hz and its harmonics to remove the power line interference.

Time frequency analyses

As in the previous study, data was segmented in trials starting at fixation onset and ending 500ms after the stimuli disappearance. 52 Missed trials (no response) and 3 trials with a RT inferior to 500ms were excluded from the analysis. We performed time frequency analysis, using Fieldtrip in Matlab, focusing on two specific frequency bands: theta (4-7 Hz) and gamma (70-120 Hz) based on their implication conflict processing and cognitive phenomena (Oehrn et al., 2014; Tang et al., 2016).

Two different methods were used to adapt to these frequency bands and get reliable power estimates. To estimate low spectral power (4 to 30 Hz), we used similar methods as the one reported in the previous Chapter. We used a sliding window of 500ms on our defined epoch and baselined using the 500ms window preceding stimulus onset. Time frequency analysis was performed using shorttime Fourier transform (STFT) in steps of 3.9 ms with a single tapper (Hanning). For the high-frequency band, spectral power was estimated from 32 to 256 Hz using an adaptive multitaper method based on discrete prolate spheroidal sequences (DPSS, aka. Slepian sequences) (Mitra & Pesaran, 1999; Slepian & Pollak, 1961). Data was baseline corrected with the median of power extracted from the 500ms prior to stimulus onset. For our analysis, we used custom made code to achieve the highest flexibility in adjusting the temporal and frequency smoothing for each frequency independently. Following this approach, we sought to find the best temporal resolution at lower frequencies, while obtaining more accurate power estimates at typically low SNR (signal-to-noise ratio) higher frequencies, at the expense of temporal and frequency resolution. As suggested by previous literature (Buzsáki & Draguhn, 2004; Hipp et al., 2012), both the mean frequency and bandwidth of meaningful brain activity typically follow a logarithmic

alaatrada	1	stimulus-locked		response-locked						
electrode localisatio	localisation	time start	time end	statistics	<i>p</i> -value	time start	time end	statistics	p-value	
theta (4-7 Hz)										
FAIL 1	MCC	0.414	0.664	-152	.029	-0.363	-0.074	-169	.016	
FAIL 10	Precentral	0.375	1.043	-565	.003	-0.406	0.200	-562	<.001	
FAIL 12	Precentral	0.391	1.100	-1097	<.001	-0.371	0.200	-944	<.001	
FAIL 13	Precentral	0.383	1.100	-1371	<.001	-0.391	0.200	-1190	<.001	
FAIL 14	Precentral	0.430	1.100	-1371	<.001	-0.340	0.200	-742	<.001	
FAS 1	SMA	0.191 0.481	0.379 0.703	138 -162	.040 .028	-0.648	-0.539	62	.088	
FAS 2	SMA	0.734	0.910	110	.037	-0.703	-0.563	89	.057	
FAS 4	SMA	-	-	-	-	-0.727	-0.644	44	.110	
FAS 5	SMA	-	-	-	-	-	-	-	-	
gamma (70-120 Hz)										
FAIL 1	MCC	0.117	0.461	640	<.001	-0.848 -0.101	-0.211 0.160	725 -301	<.001 <.001	
FAIL 10	Precentral	0.059	1.098	3104	<.001	-0.8711	0.200	3133	<.001	
FAIL 12	Precentral	0.070	0.813	1769	<.001	-0.836	0.078	1840	<.001	
FAIL 13	Precentral	0.141	0.715	833	<.001	-0.664	0.082	883	<.001	
FAIL 14	Precentral	0.141	0.543	559	<.001	-0.648	-0.109	532	<.001	
FAS 1	SMA	0.180	1.100	2656	<.001	-0.715	0.200	2759	<.001	
FAS 2	SMA	0.168	0.842	1292	<.001	-0.650	0.043	1402	<.001	
FAS 4	SMA	0.090	0.883	2615	<.001	-0.813	0.090	2875	<.001	
FAS 5	SMA	0.133	0.957	2331	<.001	-0.789	0.102	2474	<.001	

progression. Low frequency activity (theta, alpha, beta) is thought to be oscillatory, frequency-specific, and less spatially localised, reflecting a sum of different contributions, in particular widespread postsynaptic potentials. On the other hand, high frequency activity (gamma, high-gamma and above) has a broadband profile and is typically thought to reflect locally synchronous neuronal activity. However, the specific frequency range of such activity is not well established and can vary depending on the recording technique (Buzsáki & Draguhn, 2004).

To consistently capture the specificities of middle and high frequency activity, we computed power estimates across 13 logarithmically scaled frequencies FOI from 32 to 256 Hz, (i.e., each frequency was obtained by multiplying the previous one by $2^{0.25}$). In addition, we adjusted the spectral smoothing parameter to a spectral resolution of [FOI - 0.4 * FOI, FOI + 0.4 * FOI] for each frequency of interest FOI. Time windows were adjusted to include 15 cycles of FOI, using shorter windows for larger frequencies. Independent power estimates were obtained by projecting the signals onto each taper. Then, single-taper estimates were averaged across tapers, thus obtaining a single power time course for frequency.

Statistical inference of task-related activations

We focused our analyses on two electrodes localised in the frontal region (FAIL and FAS, see Table 1). In our frequency bands of interest (theta: 4-7 Hz and gamma: 70-120 Hz), we identified consecutive time points for which the power significantly differed from the baseline using t-tests with Monte-Carlo multiple comparisons correction.

Statistical inference of activations related to increased cognitive control signalling

We sought to identify electrodes responsive to indicating heightened cognitive control demand, gauged by amplified MFT power in the price minimisation task using scalp EEG recordings (refer to Chapter I). To achieve this, we compared various experimental conditions to examine a sensitivity tailored to: (1) conflict (correct incongruent vs. congruent trials), (2) error (incorrect vs. correct trials) and (3) expected loss (trials with large vs. small price difference - ΔP). To ensure consistency despite differences in response times (RT) between the experimental conditions, these analyses were conducted response locked.

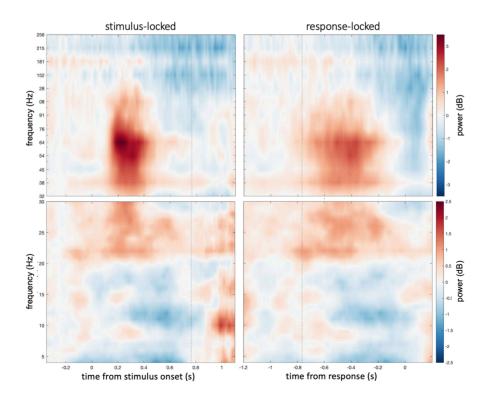
Results

Behavioural analyses

The participant's preferences did not exhibit any significant correlation with the estimated prices (tau=-.06, p=.22) (no preference-for-expensive bias) or with the price estimation error (tau=-.04, p=.43).

The participant's behaviour at the price-minimisation task (binary choices) tally with results observed in the population of healthy participants previously reported (see Chapter I). Specifically, accuracy demonstrated an increasing trend with ΔP (in euros) across different ranges ([0,1]: .50, (1,2]: .66, (2,3]: .70) and RT exhibited a decrease (mean±s.d. in seconds, [0,1]:.78±.14, (1,2]: .76±.14, (2,3]: .75±.14), confirming that trials with larger ΔP are perceived as

easier. The influence of congruency on accuracy was also apparent, as faster decisions (categorised by median split on RT) showed greater accuracy in congruent trials (proportion of correct answers: .71) compared to incongruent trials (.67). Conversely, slower decisions demonstrated the opposite pattern, with congruent choices (.62) showing lower accuracy than incongruent choices (.72). Response time was additionally affected by the participant's preference, as correct congruent trials (mean±s.d. in seconds, C_+ : .75±.14, C_- : .76±.13), while incorrect congruent trials exhibited slower responses than incongruent trials (C_+ : .80±.14, C_- : .73±.13). In essence, preferred items were consistently selected more rapidly compared to non-preferred items.



Identification of task-sensitive response in frontal electrodes

Figure 3. Example of time-frequency analyses of the electrode FAIL1, close to the MCC. Time-frequency analyses of low frequencies (4-30 Hz – lower panels) and high frequencies (32-256 Hz, log-scale – upper panels) either locked to the stimulus onset (left panels) or the response (right panels). On the x-axis, 0 indicates stimulus onset and response respectively. Dashed vertical lines mark the participant averaged reaction-time and stimulus onset, respectively.

We initially examined whether the oscillatory activity of electrodes situated in the frontal cortex showed modulation in response to the task through time-frequency analyses. These analyses were aligned with both the stimulus and the response (example of the electrode situated in the MCC – Figure 3). The findings indicated heightened gamma activity following stimulus presentation and preceding the response across all electrodes (Table 2 and Figure 5, a pattern consistent with previous observations in frontal regions (Tang et al., 2016; Bartoli et al., 2018). We observed that, in the electrode in the MCC, this increase in gamma activity was much more constrained in time (from 117ms until 461ms after stimulus onset) compared to the other electrodes for which the gamma enhancement lasted longer (see Table 2). Additionally, we found a decrease in gamma activity post response only in the MCC, suggesting that the activity recorded at this site may be very specific to the ongoing task.

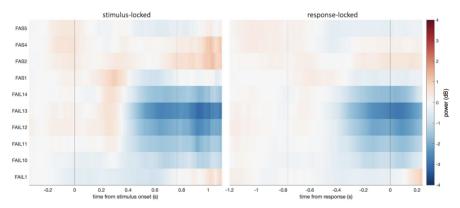


Figure 4. Task sensitive theta activity. Theta power (4-7 Hz) in decibels (dB) depending on the time from stimulus onset (left panel) or from the response (right panel), including only correct trials. The dotted vertical line represents the averaged reaction time.

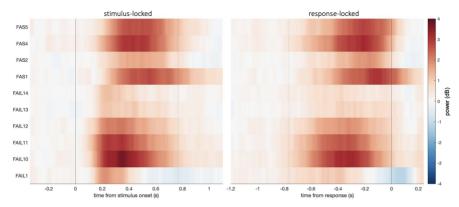


Figure 5. Task sensitive gamma activity. Gamma power (70-120 Hz) in decibels (dB) depending on the time from stimulus onset (left panel) or from the response (right panel), including only correct trials. The dotted vertical line represents the averaged reaction time.

Table 2. Electrodes' sensitivity to the task. For each time point, the observed activity is tested using two-tailed one sample t-tests from -250ms to 1100ms relative to stimulus onset (stimulus locked, left part) and from -1100ms to 200ms relative to the response (response locked, right part). Consecutive significant comparisons (for alpha=.05) of at least 100ms were corrected using Monte-Carlo multiples comparisons correction. Times at which a significant cluster starts and ends are reported, as well as the sum of the *t* statistics of the cluster and its adjusted *p*-value. A negative *t* statistics implies a decrease in the oscillatory activity compared to the baseline, whereas a positive *t* statistics implies an increase.

In the theta band, however, outcomes were less uniform between the stimulus-locked and response-locked analyses. Substantial reductions in theta power were solely evident in both analyses for electrodes localised in the precentral gyrus and the MCC (Table 2 and Figure 4. Nevertheless, except for the electrode near the MCC, the observed decline in theta power persisted postresponse, implying that these activities might not directly be associated with the decision-making process. Additionally, theta power was found to increase after stimulus onset in classical conflict tasks (Stroop, Tang et al., 2016; Bartoli et al., 2018), which further suggests that the theta modulation observed may not be related to the decision process.

Cognitive control sensitive responses in the frontal cortex

Our subsequent analysis aimed to investigate if the oscillatory activity of the task-sensitive electrodes was influenced by alterations in cognitive demands. To explore this, we conducted three comparisons: incongruent versus congruent trials, incorrect versus correct trials, and trials with large versus small ΔP . These comparisons were associated with heightened cognitive control signalling linked to conflict monitoring, error assessment, and expected loss, respectively. However, none of these comparisons revealed any statistically significant differences that withstood multiple comparison corrections. Below, we discuss potential explanations for this lack of positive results.

Discussion

The aim of this study was to explore the brain networks responsible for heightened MFT power linked to increased cognitive control demands observed in our prior research (Chapter I).

We successfully demonstrated that our analysis pipeline can be applied to iEEG data to identify areas modulated by a cognitive task like ours in an exploratory fashion. Specifically, we employed diverse time-frequency analyses for low and high frequencies to capture their distinctive features, prioritising sensitivity over spectral resolution for higher frequencies. We identified frontal regions responsive to the task, modulated at low (theta) and high frequencies (gamma), notably the MCC whose activity was modulated in both frequency ranges. In comparison to scalp EEG recordings, iEEG enabled to access localised activity in deep brain structures and explore high frequency neural activity that may provide valuable insights about the underlying neural networks and dynamics. Overall, our successful implementation of the price minimisation task with unique patients in a clinical setting lays the foundation for potential future collaborations.

Nevertheless, the study encountered significant limitations, primarily attributable to the restricted dataset and the placement of electrodes. These electrodes were indeed not positioned in brain regions typically associated with generating MFT, notably the dACC and dlPFC. The constraints encountered here are prevalent in iEEG studies, where electrode implantation, specific to each patient, hinders comprehensive comparisons between individuals and generalisations concerning the roles of specific brain areas. Studies attempting to pinpoint the sources of cognitive control signalling using iEEG recordings grapple with this challenge, revealing inconsistencies. For instance, while consistent enhancements in gamma band activity associated with conflict in the cingulate cortex and dlPFC have been noted, contradictory results concerning theta oscillations have emerged, displaying either increased or decreased theta power in these regions and differences in the strength of gamma-theta coupling (Oehrn et al., 2014; Tang et al., 2016; Bartoli et al., 2018), raising questions about the hypothesis that conflict resolution is facilitated by the coordination and integration of activity across distributed cortical networks (Canolty et al., 2006; Womelsdorf et al., 2010; Cavanagh & Frank, 2014). Moreover, a recent study demonstrated that modulations in iEEG activity in prefrontal structures in response to conflict are task-specific (Xiao et al., 2023) and suggests that cognitive control processes recruit networks which are distributed and specific to the task at hand rather than a single brain region.

Interpreting and comparing these findings remains challenging due not only to the often limited iEEG data collection, sometimes restricted to a few electrodes in areas of interest but also due to the use of varying nomenclatures, brain atlases, and analytical methods. These include differences in signal characterisation (referential or bipolar montages), utilisation of single electrodes versus averaging across several, variations in the definition of frequency ranges, specifically gamma, and several choices regarding time-frequency decomposition (sliding-window Fourier, wavelet or multitaper methods, time and frequency smoothing parameters which affect signal to noise ratio and resolution). Future research is necessary to unify these findings and clarify the neural mechanisms underpinning the detection and resolution of conflict. Moreover, exploring heightened cognitive control across various scenarios (such as error monitoring or expected rewards) within the same individuals is essential to advance our understanding of the generality and specificity of these phenomena. Given its better characterisation in scalp EEG recordings, measuring simultaneously both scalp and intracortical potentials would also be beneficial in comprehending how neural signals, particularly slow-frequency activity, translate across different scales.

Finally, the inconsistencies observed in previous iEEG studies may signify mechanisms that might not be discernible through a mere increase in localised brain activity. Instead, they could be identified through distinctive synchronisation patterns of brain rhythms across a broadly distributed prefrontal-cingulate network.

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