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Bayesian Account of Perceptual Decision-Making

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Bayesian Account of Perceptual Decision-Making

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Abstract

By making predictions, learning from mistakes, and updating memories to include new information, the brain enables adaptive behaviour in daily activities. For instance, in perceptual decision-making tasks, it is critical to rapidly select the best behaviours based on current sensory inputs, that are frequently ambiguous or masked by noise. Using random dot motion (RDM) tasks, previous research on perceptual decision-making emphasised the role of sensory information in directing behaviour by varying simply the stimulus coherence and analysed the data using models that more or less explicitly presuppose bottom-up processing (e.g., drift-diffusion models). However, accumulating evidence (e.g., Bayesian models and the Free Energy Principle applications) suggests that the brain approximates optimal Bayesian inference rather than simply being a passive information filter. As a result, we need to shed light on the computations involved in goal-directed decision-making, with a focus on the predictive mechanisms at work in volatile experimental contexts. Here we used a probabilistic Random Dot Kinematogram (pRDK) in which the probability of witnessing a rightward/leftward motion changes throughout the task. Furthermore, to operationalise the predictions of the left and right dot motion in each trial based on previous information, an Ideal Bayesian Observer was used. This allowed us to study top-down predictions' impact on decision-making. The behavioural analyses revealed a substantial impact on behaviour from both coherence levels and probabilistic contexts. Specifically, a significant interaction between the probability of motion and direction was found, indicating faster responses when predictions matched what was presented.

Keywords: Perceptual decision-making, Bayesian Inference, Random Dot Motion, Top-down predictions

1 Introduction

1.1 Decision-Making

In the realm of human cognition and behaviour, decision-making stands as a cornerstone process that shapes our lives in multifaceted ways. Every day, individuals confront a myriad of choices, ranging from the mundane to the life-altering, and the process of decision-making is what enables us to navigate these choices effectively. Whether it is choosing between a healthy salad or a tempting burger for lunch, deciding on a career path, or making complex financial investments, our decisions reflect the intricate interplay of various cognitive, emotional, and situational factors. Indeed, decision-making is a pivotal skill that plays a central role in daily life, empowering individuals to adapt to their environment and exercise personal autonomy (Morelli et al., 2022). Hence, gaining insight into the mechanics and neural underpinnings of this ability has become crucial. As a consequence, multiple scientific

disciplines, including cognitive psychology and neuroscience as well as economics, computer science, and neuropsychology, have extensively studied decision-making, employing various theoretical models as references (Broche-Pérez et al., 2016; Edwards, 2000; Tversky & Kahneman, 1977, von Neumann and Morgenstern, 1944).

In cognitive neuroscience and psychology, decision-making can be defined as a multifaceted executive function (Rosenbloom et al., 2012) that involves the cognitive processes of evaluating and selecting a stimulus or course of action from a range of possible alternatives (Broche-Pérez et al., 2016; Morelli et al., 2022). Thus, it consists of the mental operations through which individuals make choices based on available information, preferences, goals, and potential outcomes (Doya, 2008; Morelli et al., 2022). Ernst & Paulus (2005) have proposed a fundamental framework for decision-making organised around an input–process–output–feedback structure and encompassing well-defined stages: (a) presentation of multiple stimuli that predict measurable outcomes (*input*); (b) evaluation of the various options and the establishment of preferences (*process*); (c) selection of actions based on the presented stimuli (*output*); (d) assessment of the outcomes which provides valuable feedback to refine future decision-making (*feedback*).

Decision-making can be based on individual preferences and beliefs (*value-based decision-making*) or objective characteristics (*perceptual decision-making*). Thus, two different types of decision-making can be distinguished: value-based and perceptual decision-making.

1.1.1 Value-based decision-making and its neural correlates

Theoretical frameworks, such as the Expected Utility Theory[1] (Von Neumann & Morgenstern, 1944), Prospect Theory (Kahneman & Tversky, 1979)[2], and computer science's reinforcement learning (RL) theories (Sutton & Barto, 1998), appear to share a common argument: decision-makers combine the different characteristics of a choice to derive a single measure of its subjective value and then select the most valuable option. Furthermore, this process is often

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[1] Each possible outcome is assigned a numerical value representing the likelihood of occurrence (i.e., expected utility).

[2] The work of Kahneman and Tversky on the psychology of valuation and choice emphasises the importance of intuitive over deliberative decision-making and challenges basic economic assumptions of rationality. Thus, individuals are more risk-averse when provided with decisions presented as losses, but they are more risk-averse when presented with decisions framed as profits, giving the two options equal value.

influenced by factors such as reward expectation, risk aversion, and the integration of value-related information (Doya, 2008).

From an anatomical perspective, value-based decision-making involves intricate interactions among multiple brain regions that encode, represent, and process subjective values. Two brain regions that were associated with value-based decision-making are the orbitofrontal cortex (OFC) and the anterior cingulate cortex (ACC). In addition to encoding and representing the subjective worth of various options, the OFC processes reward-related characteristics and guides decision-making based on reward expectancy and outcome valuation (Broche-Pérez et al., 2016; Roesch & Olson, 2005; Wallis, 2007). Moreover, the OFC's bidirectional connections with the temporal sensory association cortex, amygdala, and hippocampus enable emotional processing (Broche-Pérez et al., 2016). The OFC also interacts with the basal ganglia, providing support for reward-related learning, as these regions are part of the striatal dopamine system (Krawczyk, 2002). However, it is important to note that the OFC is not the sole brain region responsible for reward processing. Indeed, Doya's review (2008) reveals that, when a high reward is expected, individuals tend to choose an action despite the presence of a considerable cost. This behaviour is linked to dopamine-mediated activity in the ACC. Additionally, the ACC, along with the ventral striatum (Hare et al., 2008), has been found to encode prediction errors[3] with activity increasing in response to mistakes and positive feedback (Morelli et al., 2022). These findings highlight the involvement of multiple brain regions, including the OFC, ACC, and ventral striatum, in the complex process of value-based decision-making.

As mentioned earlier, the OFC and the ACC are intricately connected to the dopaminergic reward circuit, contributing to decision-making processes at various levels, including pleasure (reward-driven approach), subjective value (value-based decision), and goal-directed control (Doya, 2008). Early investigations by Schultz (1997) have already laid the groundwork by demonstrating that dopaminergic neurons encode a reward prediction error signal, aligning with the concepts proposed by temporal-difference learning models (TD-models[4], Sutton & Barto, 1998). Subsequently, numerous pieces of evidence have consistently supported these

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[3] Prediction errors refer to the discrepancy between expected and actual rewards or outcomes; they are positive every time something better than expected happens, and negative when the opposite occurs (Schultz et al., 1997; Sutton and Barto, 1998).

[4] TD-models assume that the agent predicts and evaluates future rewards based on the difference between the predicted and actual rewards obtained during interactions with the environment at different time steps.

findings, suggesting that dopaminergic neurons in the midbrain carry a "teaching signal", facilitating the learning of the subjective value of actions (Sharpe & Schoenbaum, 2018).

1.1.2 Perceptual decision-making and its neural correlates

While value-based decision-making relies on *subjective* preferences, perceptual decision-making involves the integration of *objective* sensory information to make judgments about the external world (Hauser & Salinas, 2014). It is grounded in objective perceptual data, where incoming sensory signals are gathered through the senses, evaluated and interpreted to determine the most suitable response.

Perceptual decision-making is a complex cognitive ability that hinges on a dynamic interplay of both bottom-up processes, involving the representation of sensory evidence, and top-down processes, encompassing the integration of this sensory evidence (Hauser & Salinas, 2014). A consensus among several studies highlights the presence of two foundational principles underpinning this intricate capacity: (1) perceptual competition (Gold & Shadlen, 2001; Hauser & Salinas, 2014) and (2) the accumulation of evidence (Gold & Shadlen, 2007). The principle of perceptual competition (1) establishes a relationship between the choice made and specialised sensory neurons tuned to attributes characteristic of each decision option (Gold & Shadlen, 2001; Heekeren et al., 2008). According to the accumulation of evidence framework (2), on the other hand, a decision involving two alternatives unfolds through the parallel accumulation of corresponding evidence, ultimately culminating in a response as soon as one of the decision thresholds is hit. Thus, Reaction Times (RTs) denote how long it takes for a decision signal to be accumulated until a certain threshold is reached, triggering a response. A compelling illustration of this hypothesis is evident when examining responses to noisy psychophysical stimuli such as a Random Dot Kinematogram (RDK, i.e., a typical stimulus used to study motion perception; see details below). Drift-diffusion and sequential sampling models (Ratcliff & Smith, 2004), as well as some Bayesian models (e.g., Bitzer et al., 2014) encapsulate this process of information accumulation, offering a foundation to comprehend perceptual inference in an environment characterised by sensory uncertainty.

Consistently, in real-life scenarios, the information at hand is often laden with noise and uncertainty, necessitating the engagement of decision-making and inference processes. Consider a situation where we encounter a person on the street and need to determine if we know him\her or not. On a clear day, effortlessly, we can discern whether the person is familiar

or a stranger and promptly decide whether to greet or ignore him\her. However, during a rainstorm, the sensory input becomes noisier, requiring us to observe for a longer duration to gather more sensory data for deciding about the person's identity and selecting an appropriate behavioural response. This type of decision-making process is essential not only for everyday situations, like the one described above, but also for more biologically and socially significant circumstances (Heekeren et al., 2008). Interestingly, the source of the noise is not solely external but can also emerge from the sensory system itself. While RT durations have conventionally been associated with information accumulation, some researchers have proposed that the observed variability in RTs stems from internal sensory and neural mechanisms (Genest et al., 2016). To investigate this hypothesis, Genest and colleagues (2016) employed a Random Dot Tachistogram task. A spatially randomised array of dots is very briefly presented, followed by a single displacement to the left or right (as opposed to the continuous and longer movement seen in RDK). Consequently, this task necessitates the rapid integration of information occurring virtually instantaneously, precisely at the moment of transition between dot positions. The findings reveal that, although this stimulus does not introduce a consistent flow of noise (temporal noise) into the decision-making system as the RDK does, it still induces variability in RTs. This observation reinforces the notion that such variability originates intrinsically within the system itself (Genest et al., 2016).

Another model that puts forth hypotheses regarding the mechanisms underlying perceptual decision-making is the one by Sugrue et al. (2005). Initially, a sensory transformation occurs, translating primary sensory input into a representation of a more complex stimulus aspect (e.g., visual motion). Subsequently, a decision transformation establishes a connection between this sensory representation and the likelihood of various possible responses. The conclusive phase of processing culminates in the concrete binary decision, transforming the continuous probabilistic representation into the execution of motor actions. However, as demonstrated in a study conducted by Heekeren et al. (2008), the mechanism underlying perceptual decision-making does not conform to a solely *hierarchical* model unfolding in a linear progression of perception, decision, and action implementation. Instead, it can be better understood as a system comprising four discrete neural processing modules, forming a *heterarchical* architecture (shown in <u>Fig. 1</u>). The initial module is crucial for the *accumulation* and *representation of sensory evidence* (such as the Middle Temporal, MT, area for motion perception). The second module is responsible for identifying *perceptual uncertainty* or difficulty and signalling the need for increased attentional resources to accurately implement a

task (associated with regions like the anterior insula and inferior frontal gyrus). The third module encapsulates the *representation of decision variables*[5] including structures such as the dorsolateral prefrontal cortex (DLPFC) and encompasses motor and premotor regions. Lastly, the fourth module is dedicated to *performance monitoring*, detecting errors and recognizing when adjustments in decision strategies are essential to optimise the overall performance. The principal brain area associated with error monitoring is the posterior medial prefrontal cortex (pmPFC). Its activity was related to detecting discrepancies between intended outcomes and actual results, allowing individuals to rectify mistakes and enhance future performance (Ridderinkhof et al., 2004).
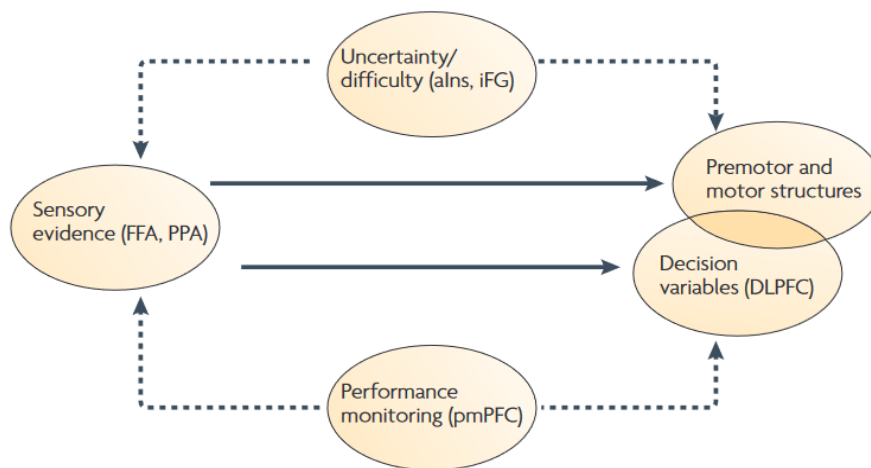

Figure 1 | Heterarchical architecture of the four neural models underlying perceptual decision-making (Heekeren et al., 2008). [FFA: fusiform face area; PPA: parahippocampal place area; DLPFC: dorsolateral prefrontal cortex; aIns: anterior insula; iFG: inferior frontal gyrus; pmPFC: posterior medial prefrontal cortex].

Consistently, a wealth of evidence supports the involvement of the lateral prefrontal and parietal cortex in the selection and execution of choices from a range of available alternatives (Gold & Shadlen, 2007; Kable & Glimcher, 2009, 2009; Schall, 2001). More specifically, the DLPFC emerges as intricately tied to decision-making processes (Philiastides et al., 2011), assuming a specialised role in integrating diverse information sources and exercising cognitive control (Kim & Shadlen, 1999; Rosenbloom et al., 2012). In parallel, the posterior medial frontal cortex appears implicated in performance monitoring and error detection (Heekeren et al., 2008; Ridderinkhof et al., 2004), elucidating its contribution to evaluating outcomes and detecting discrepancies.

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[5] The decision variable is a composite measure that integrates various sources of information, including prior knowledge, sensory evidence, and subjective value, into a single quantity. This quantity is then used by a decision rule or process to make a choice or decision (Heekeren et al., 2008).

Ever since the notion that decision-making involves intricate mechanisms connecting sensation and action (rather than simple reflexes) emerged, neurophysiologists have diligently sought to comprehend the formation of these links and the transformative processes involved (Shadlen & Gold, 2004). Initially, this endeavour led to the investigation of the visual and oculomotor systems in the primate brain. One of the pioneering demonstrations showcasing the correlation between the activity of individual cortical neurons and perceptual decisions resulting in actions was conducted by Shadlen & Newsome (1996). Their study has illustrated that specific neurons in monkeys' lateral intraparietal area (LIP) conveyed signals seemingly reflecting the integration of sensory information, leading to a decision suitable for guiding movement. Firstly, LIP neurons receive significant input from direction-selective neurons in the MT area, indicating a flow of information related to motion processing (Hauser & Salinas, 2014; Lewis & Van Essen, 2000). In this case, LIP is regarded to be critical for integrating the noisy MT outputs across trials, resulting in a more accurate decision (Shadlen & Newsome, 1996). Secondly, LIP neurons project to the superior colliculus and the Frontal Eye Fields (FEF), which are responsible for generating movements, especially in the context of eye movement responses (Hauser & Salinas, 2014; Heekeren et al., 2008; Paré & Wurtz, 1997; Shadlen & Newsome, 1996). Lastly, many LIP neurons show sustained and spatially selective activity when a monkey is instructed to make a delayed eye movement, suggesting their involvement in decision-related processes and working memory (Lewis & Van Essen, 2000; Shadlen & Newsome, 1996). These findings collectively support the role of the LIP as a critical neural hub for motion-related decisions.

1.1.3 Random Dot Kinematogram (RDK) task

To investigate perceptual decision-making, researchers have primarily employed two alternative forced-choice paradigms (Hauser & Salinas, 2014) where the subject must use available sensory information to give a dichotomous response. The probably most utilised task, in both humans and nonhuman primates, is the Random Dot Motion (RDM). Random Dot Motion is a broader term that refers to any visual stimulus involving randomly moving dots. It includes the concept of Random Dot Kinematogram (RDK) but is not limited to that specific experimental design. In an RDK task, participants typically have to discriminate a cloud of moving dots according to whether it moves in one of two opposing directions (Britten et al., 1992; Pilly & Seitz, 2009) and express their decision through eye movements or motor responses. To manipulate the level of difficulty and sensory uncertainty, the coherence of the

dot motion is often varied (from weak to strong strength of motion[6], as illustrated in <u>Fig. 2</u>). Coherence refers to the proportion of dots that move in a consistent direction, while the remaining dots move randomly (referred to as noise dots). For example, for a 25% level of coherence, only 25% of the dots move in the same direction while the other 75% of the dots (i.e., noise dots) move in random directions.
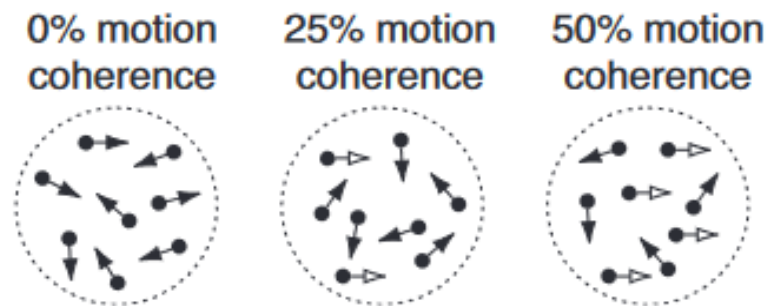

Figure 2 | A random-dot motion stimulus with different levels of motion coherence (Palmer et al., 2005). No dots are moving in the same direction when the motion coherence is 0%. As the percentage of coherent dots increases (e.g., 25% and 50% motion coherence), the global motion becomes less noisy, and detection or discrimination performance improves with higher accuracy and shorter Response Times.

As one would expect, higher coherence levels make it easier for participants to perceive the global motion direction, while lower coherence levels introduce more ambiguity\uncertainty, thus subjects respond slower and make more errors (Gold & Shadlen, 2007; Palmer et al., 2005; Shadlen & Gold, 2004). Although the RDK task may appear as an oversimplified representation of how our brain processes continuous, complex sensory input and categorises it into multiple distinct categories, this task has yielded a plethora of valuable insights into the mechanisms underlying perceptual decision-making (Heekeren et al., 2008).

As mentioned earlier, a critical characteristic of the RDK tasks is the deliberate introduction of a level of sensory noise in the stimuli. Historically, one way to quantify the decision formation about noisy sensory signals involves the trade-off between speed and accuracy. Deciding quickly can lead to the risk of overlooking essential information while taking more time allows for the acquisition of additional or higher-quality signals, but it may result in time being wasted. To measure how the level of noise influences the subjects' RT and accuracy, stimuli strength (i.e., coherence) can be varied from trial to trial so that the proportion of correct response and the mean RT can be plotted as a function of this strength (Palmer et al., 2005).

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[6] Weak and strong strength of motion refer respectively to the majority of dots moving in a random direction or to the majority of dots moving coherently in a single direction.

To visualise this kind of relationship, one can create a *chronometric function* (measurements of RT as a function of stimulus strength) and a *psychometric function* (measurements of the proportion of correct response as a function of the stimulus strength) illustrated in Fig. 3.
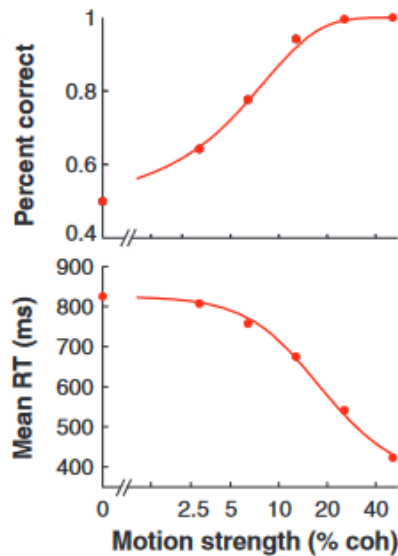

Figure 3 | The impact of motion coherence on accuracy and mean RT (Gold & Shadlen, 2007). The proportion of accurate responses on a log scale is shown in the top panel (psychometric function), and the mean RT for correct responses is shown in the bottom panel (chronometric function).
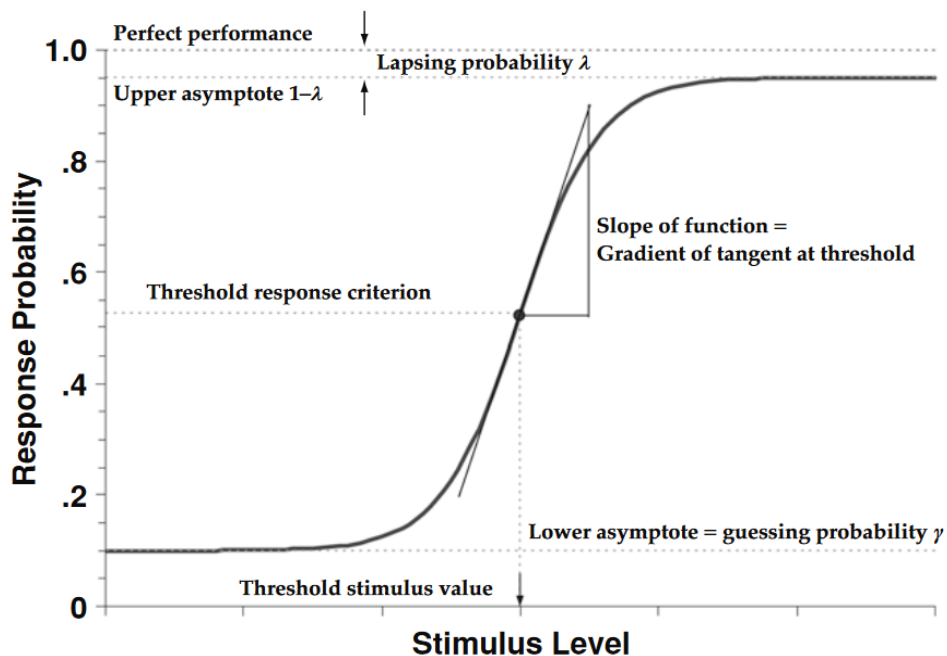
Figure 4 | The psychometric function is defined by four key parameters: the threshold, slope, upper asymptote, and lower asymptote. Performance at lower stimulus intensities is defined by the lower asymptote. Meanwhile, the slope parameter, which typically represents the gradient at the threshold point, determines the rate of change in response probability per unit of variation in stimulus level (Gilchrist et al., 2005). The sensitivity threshold refers to the minimum level of stimulus intensity or information required to trigger a response or detection in a sensory or decision-making system *(Kontsevich & Tyler, 1999).*

It is important to note that psychophysical experiments utilise the psychometric function (whose parameters are depicted in Fig. 4) because it enables the description of the transition from non-detectability to detectability in a gradual manner. What is particularly informative is the slope of this function and not only the sensitivity threshold (Gilchrist et al., 2005; Kontsevich & Tyler, 1999). Indeed, in the study presented in this thesis work, an adaptive and Bayesian procedure was used to estimate the psychometric slope and threshold of each subject (see adaptive phase in the method section).

The Signal Detection Theory (SDT) is a valuable conceptual framework employed in experiments involving this type of stimulus manipulation. It facilitates the interpretation of how stimulus strength influences accuracy performance (Gold & Shadlen, 2007; Green & Swets, 1966). According to SDT, decision-makers receive evidence information (e)[7], which is often derived from sensory inputs in perceptual psychophysics experiments. This evidence is influenced by both the manipulated state of the stimulus (e.g., its absence or presence, as controlled by the experimenter) and by noise inherent in the system. As a result, "e" becomes a random variable, described through conditional probability distributions (Gold & Shadlen, 2007), such as the likelihood of the evidence (e) given a specific alternative or hypothesis (h), denoted as $P(e|h)$. The decision is made by comparing a sample from this random variable to a criterion (Gold & Shadlen, 2007; Palmer et al., 2005). Thus the objective is to ascertain which hypothesis or alternative is responsible for generating the observed evidence. Even though SDT is a strong analytical tool, early research was limited owing to the need for more powerful computers (Hauser & Salinas, 2014). On the other hand, modern research frequently integrates psychophysical findings with concurrent neurophysiological data from the same individual, augmented by comprehensive computer analysis and model simulations. This integrated approach allows for the introduction of the so-called *drift-diffusion* model (Palmer et al., 2005; Ratcliff & Smith, 2004).

1.1.4 Accumulation of evidence in bottom-up models of perceptual decision-making

Ratcliff's (1978) diffusion model technique has shown to be particularly effective in explaining RT and accuracy data in two-choice RT tasks. For instance, this modelling approach has

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[7] In this context, by "evidence," I am referring to information that guides us in determining when or whether to commit to a specific option.

successfully accounted for phenomena such as the distribution of RTs heavily skewed toward longer durations and the intricate balance between speed and accuracy (Bogacz et al., 2006). Diffusion models propose that decisions are formed by continuously accumulating sensory information until an upper or lower bound is hit, which triggers a response (Heekeren et al., 2008; Palmer et al., 2005; Voss et al., 2013). This accumulation of information begins at the starting point and can be considered as a counter running in a corridor between the two bounds and pushed in opposing directions by information supporting one alternative rather than the other (Voss et al., 2013). In more technical terms, noisy momentary evidence favouring one or the other alternative displaces a decision variable (DV) in either a positive or negative direction. However, due to random noise, the trajectory of the decision path (as depicted in Fig. 5) varies from trial to trial with a random fluctuation (Voss et al., 2004, 2013). In addition, the momentary evidence is distributed as a unit-variance Gaussian whose mean is proportional to the coherence of the stimulus (Doya et al., 2006). Thus, in a basic diffusion model, such as the one depicted in Fig. 5, the characterization of performance involves several key components. These components comprise an initial *starting point* (depicted as '0' in Fig. 5), which serves to accommodate any pre-existing biases within the decision-making process. Additionally, a *drift rate* parameter (represented as 'μ' in Fig. 5) is employed to quantify the speed at which information is assimilated, as established by Voss et al. in 2013. Furthermore, distinct *bounds* are established for each available alternative, denoted as 'A' and '-A' in Figure 5.
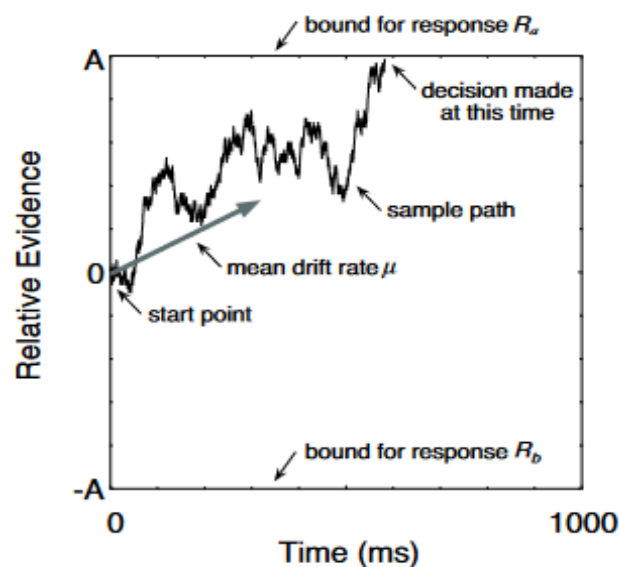

Figure 5 | Illustration of a simple drift-diffusion model (Palmer et al., 2005). The drift-diffusion parameters are the starting point (at 0), mean drift rate (μ) and a bound for each response (A and -A).

As indicated before, by adjusting the starting point, it is possible to model the response biases. This parameter encapsulates the disparity in the quantity of information required before a decision threshold is reached and a response is executed. In essence, a greater distance between the starting point and the decision threshold leads to a lengthier decision process (Voss et al., 2004). On the other hand, the drift rate indicates the relative amount of information assimilated per unit of time (Voss et al., 2004). Consequently, it can be considered as a measure of perceptual sensitivity. For instance, a clear stimulus (characterised by a low level of noise) imparts more sensory data compared to a degraded one, thus resulting in a higher drift rate.

To summarise, the brain continuously acquires a constant piece of evidence from the input, known as drift, which is subject to noise, or diffusion[8]. Hence, the evidence accumulates over time, leading the decision-maker to either commit to one of the two options or await further pieces of evidence (Doya et al., 2006). Finally, the accumulation process concludes once sufficient evidence is gathered, and the final choice is determined by the specific bound that is crossed, with the decision time dependent on the time it takes to cross that bound.

Importantly, drift-diffusion models have been employed for behavioural data and to analyse neurophysiological signals as well. For example, Gold & Shadlen (2007) delved into the neural mechanisms underlying perceptual decision-making in nonhuman primates, revealing that activity (i.e., mean firing dynamics of single neurons) in the LIP and FEF correlates with the accumulation of sensory evidence (i.e., drift-diffusion model mean trajectories) and subsequent visuo-saccadic decision-making.

Earlier research on perceptual decision-making underlined only the relevance of sensory information in driving behaviour. These studies have extensively investigated perceptual decision-making using models that implicitly or explicitly assume bottom-up processing and a simple accumulation of sensory information over time (e.g., the drift-diffusion model). However, while exploring the physical properties of a stimulus is crucial, it is equally essential to examine how other factors can impact perceptual performance. In line with this perspective, recent experiments have grown more ambitious, delving into the manipulation of reward amounts, temporal constraints (Hauser & Salinas, 2014) and reward probabilities (Behrens et al., 2007). These findings strongly suggest that sensory processing receives feedback regarding ongoing decision-making and that environmental statistics (e.g., the probability of a stimulus

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[8] Formally, diffusion is a scaling parameter, thus it is not a parameter to be estimated but it has to be fixed to any constant value (Voss et al., 2004).

occurring) also affect behaviour. Furthermore, when sensory information is noisy, expectations can influence perception, altering not just how well, but also what is perceived (de Lange et al., 2018). For instance, the perceived direction of motion can exhibit a bias induced by an implicit prediction (or equivalently here, expectation) of the most probable direction, rooted in prior trial experiences. Indeed, within the scope of this thesis, a novel version of the RDM task was employed, referred to as the probabilistic Random Dot Kinematogram (pRDK). This task introduces a dynamic element by changing the probability of witnessing rightward motion throughout the task. By doing so, we aimed to explore perceptual decision-making capacity concerning predictive processing. Our experimental setup indeed places significant emphasis on the role of predictive processing, which assumes a pivotal stance in comprehending how individuals formulate decisions by assimilating the available information and their future event expectations.

1.2 From brain as a passive filter to brain as a predictive machine

Despite the early recognition of the importance of predictive mechanisms in both psychology and neuroscience (Clark, 2013; Doya et al., 2006; Rao & Ballard, 1999), typical approaches to understanding cognitive processes have often assumed a sequential flow from sensory input to executive functions and then to overt behaviour. For a long time, the prevailing belief about the brain was that its primary role is to passively receive and process sensory information, lacking any significant role in shaping or influencing the perceived evidence. This view can be traced back to the original behaviourist ideas, which emphasised a linear progression from sensory stimulation to observable behaviour (stimulus-response). These views also had an impact on early information-processing cognitivist theories, which sought to understand how information was processed step-by-step in the human mind. Such view proposes that perceived sensory data follows a hierarchical pattern of analysis by distinct feature detectors in sequential stages. This serial processing implies that one operation must be finished before the next may begin, similar to how a computer works. Thus, the brain was often regarded as a filter, extracting essential information from sensory inputs while discarding irrelevant details. Although these models provided valuable insights at the time, contemporary research now acknowledges the brain's dynamic and interactive nature, involving feedback loops (Rao & Ballard, 1999), parallel processing (Hinton & Anderson, 2014), and complex interactions

between different brain regions. According to current views (e.g., Rao & Ballard, 1999), the brain actively predicts its sensory information and bottom-up processes encode prediction errors, namely the mismatch between the prediction and the sensory input. Indeed, when there is this discrepancy, the brain triggers responses that may involve the generation of new predictions. These updated perspectives provide a more comprehensive understanding of cognitive functioning and the brain's remarkable ability to flexibly integrate information from diverse sources (Babic et al., 2010). Moreover, scholars argue that even classical conditioning has a predictive nature (Sutton & Barto, 1981). Within the classical conditioning framework, learning entails the understanding that the occurrence of one stimulus predicts the occurrence of another. Although behaviourism, as a theoretical perspective, focuses solely on analysing explicit behaviour, a notable development emerged: the Rescorla-Wagner model (R-W model). This model introduced a mathematical representation of associative learning and was the first to propose a global error term as a fundamental element in the learning process (Soto et al., 2023). It analyses how the discrepancy between expected and actual consequences promotes learning and hypothesises how the magnitude of the prediction error affects the associations between events (Bubic et al., 2010). In other words, learning occurs when what happens differs from what is expected, underlining the importance of *surprise*[9]. Therefore, rather than passively processing sensory inputs, the brain is now understood to play a dynamic and constructive role in forming representations of the world. This perspective aligns with the concept of *predictive processing*, where the brain continually generates expectations about incoming sensory information based on prior knowledge and experience. These predictions are actively compared with the actual sensory input, allowing the brain to refine and adjust its understanding of the world in an ongoing feedback loop. As a result, we are currently witnessing a fundamental theoretical shift in neuroscience, as the prevailing view considers the brain as a predictive organ. One essential model that marks this shift is undoubtedly the Predictive Coding model.

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[9] Here surprise is intended as the difference between what really occurs and what is expected

1.2.1 Predictive Coding

Following von Helmholtz[10]'s observations (Westheimer, 2008), the predictive coding framework challenges the traditional notion that the brain constructs its understanding of the world solely by accumulating sensory information in a bottom-up fashion. The predictive Coding model indeed emphasises the relevance of predictions (or contextual information) and prediction errors in brain processing. Learning happens through prediction refinement based on sensory feedback. Thus, the brain is viewed as continually generating and updating an internal model of the environment through a reciprocal exchange of top-down and bottom-up information across multiple hierarchical levels (Friston, 2005, 2009; Rao & Ballard, 1999). Therefore, instead of directly representing visual stimuli, it is more efficient for the brain to encode prediction errors. This error signal is what gets transmitted to higher brain areas. However, when the brain's predictions match the incoming sensory information, there is no need to send signals or "spikes" to higher brain regions because everything aligns with expectations. This efficient coding strategy helps the brain conserve energy and process sensory information more effectively

Predictive coding has been applied to various domains, including vision, providing a plausible explanation for how visual responses are influenced by the context and accounting for modulatory effects beyond the traditional receptive field. The idea of predictive coding was translated into a computational model of vision by Rao & Ballard in the late 1990s (Rao & Ballard, 1999). Their model demonstrated that a generative model of a scene (top-down processing), coupled with feedback through error signals, leads to the updating and refining of predictions. As depicted in Fig. 6, each higher level attempts to predict the activity at the lower levels via feedback connections. When there is a mismatch (i.e., prediction error) between the prediction and the actual activity of the lower level, the error signal is propagated to the higher level via feedforward pathways. These prediction errors are vital because they serve as signals for the predictive estimator (PE; shown in Fig. 6), enabling it to adjust and refine its current estimate of the input signal and generate subsequent predictions accordingly (thus, "explaining away" or cancel out the prediction errors). In other words, while feed-forward connections convey input-related information, feedback activities allow the transmission of "contextual effects".

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[10] From Helmholtz comes the idea that sensory systems developed to infer the reasons for changes in sensory inputs (Clark, 2013).

This computational model aligns well with the known neuroanatomy and physiology of the visual system and also explains phenomena like extra-classical receptive field effects such as end-stopping[11] (Friston, 2005).
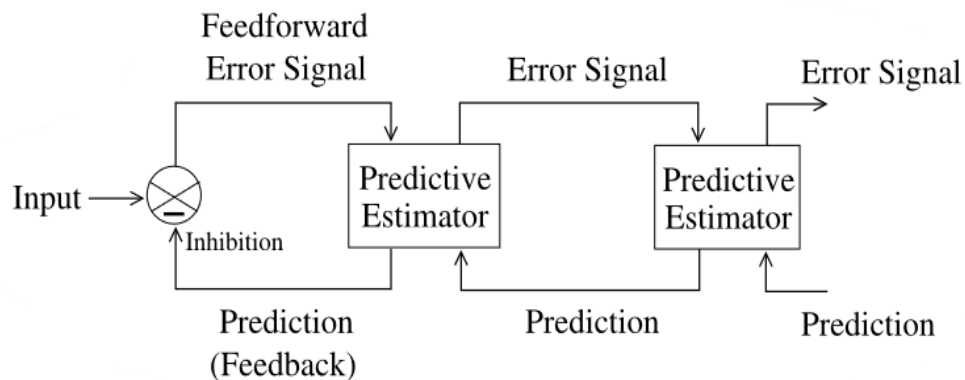

Figure 6 | Schematic representation of the hierarchical Predictive Coding Model by Rao & Ballard (1999)

However, during that time, there was a need for a more comprehensive and all-encompassing theory, especially one that could address the challenging task of modelling distal causes of sensory input as well as uncertainty. Indeed, in everyday life, we often lack complete information to fully comprehend the causes behind incoming sensory stimuli. As a result, we rely on making inferences using the limited or partial information available to us. This is where Bayesian theories come into play. The next subsection is dedicated to Bayesian theories but, in essence, these theories suggest that to forecast the future, the brain constantly updates an inner hierarchical generative model of its sensory inputs in a (roughly) Bayes-optimal fashion (Clark, 2013; Friston, 2005, 2009, 2010; Friston et al., 2017; Doya et al., 2006).

1.2.2 The Bayesian Brain Hypothesis

In recent years, an increasing body of research has embraced Bayesian models to delve into different cognitive processes (for a comprehensive and historical review, see Clark, 2013). This rise of interest stems from the understanding that the cognitive system faces the challenge of dealing with uncertainty across various experimental tasks and everyday situations. Central to this exploration is the so-called "Bayesian Brain" Hypothesis (Friston, 2005; Doya et al., 2006;

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[11] In end-stopping receptive fields the neuron's response to a visual stimulus is maximal when the stimulus is of a certain length or within a specific range of lengths. However, if the stimulus extends beyond this optimal length or size, the neuron's response decreases or even ceases altogether (Friston, 2005).

Knill & Pouget, 2004), which portrays the brain as an active inference machine adept at representing sensory information in the form of probability distributions. This probabilistic representation allows us to describe uncertainty, extending beyond the simple true/false logic to a realm of continuous plausibility. Indeed, numerous studies have demonstrated the effectiveness of Bayesian inference in modelling information processing under uncertainty (e.g., Chater et al., 2010; de Lange et al., 2018; Friston et al., 2017). Furthermore, it is essential to recognize that uncertainty is not always inherent to our physiology; rather, it may arise due to our limited knowledge or partial observations. Therefore, updating our beliefs about the environment as we gather more evidence becomes vital, and Bayesian inference serves as a powerful tool to connect the inner world models with the supporting evidence, thus accommodating prior beliefs. For example, in the context of a sensory-motor task, a prior may represent the predicted probability of encountering a specific stimulus. Certain beliefs might be ingrained since birth, while others exhibit a more adaptable nature, being formed through experiences, or even fluctuating from one trial to the next in response to shifts in sensory input (Ma & Jazayeri, 2014).

More formally, a Bayesian model necessitates the integration of four distinct components depicted in <u>Fig. 7</u> (Bitzer et al., 2014): (1) A *generative input process* responsible for the conversion of sensory input into noisy observations of the stimuli; (2) An *internal*[12] *generative model* designed to generate predictions, against which sensory samples are assessed to refine the beliefs about underlying causes generating the input; (3) a *Bayesian inference* process which allows translating noisy observations into posterior beliefs over the stimulus causes. This translation is executed using the generative models corresponding to each decision option; (4) A *decision policy* based on the posterior beliefs from the Bayesian inference.

Specifically, within cognitive neuroscience experiments, the input process (1) given to the model often comprises the experimental data themselves (Bitzer et al., 2014). Because we cannot quantify the real noisy values computed by the brain, it is assumed that they are drawn by a Gaussian distribution whose parameters are estimated using experimental data. Furthermore, the internal generative model (2), which can also be specified by a Gaussian density, characterises the estimation of how the external world generates these inputs.

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[12] This generative model is internal because it reflects the individuals' beliefs
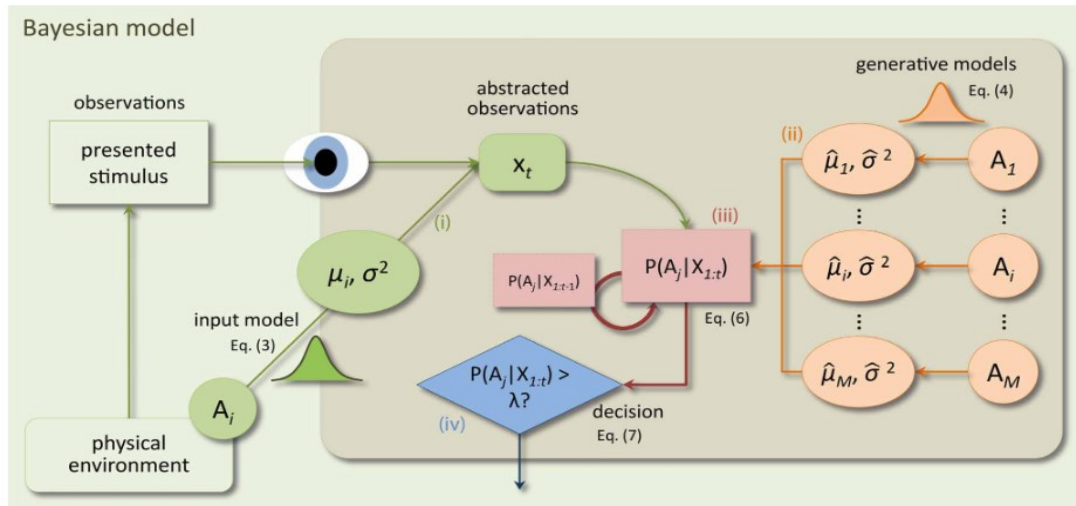
Figure 7 | A schematic diagram, following Bitzer et al. (2014), outlines a basic Bayesian model. Through sensory processes, the stimuli are transformed into abstracted observations (x_t). The input model (i) approximates this transformation by associating the decision alternative A_i (out of M alternatives) with a value x_t drawn from a Gaussian distribution. Its mean (μ_i) signifies the value derived by the brain under conditions of noise-free observations. However, real-world observations are noisy, and the variance σ^2 encapsulates the magnitude of this noise. The process of Bayesian inference (iii) operates recursively to calculate posterior beliefs, incorporating past beliefs [$P(A_j|X_{1:t-1})$] and the internal generative models (ii) associated with each alternative (out of M alternatives). Decisions are subsequently enacted using a decision policy (iv) grounded in the computed posterior beliefs and a designated threshold λ. In this particular context, the concept of a "threshold" closely resembles the boundaries used in drift-diffusion models. In this Bayesian model, decisions are reached by evaluating the posterior beliefs associated with different alternatives. When any of these posterior beliefs surpasses a predetermined threshold or bound, a decision is made in favour of the alternative with the highest posterior belief.

Thus, the generative model can be broken down into two components: the *likelihood*, representing the probability of sensory data (x) given their causes or states (s) [$P(x|s)$], and the *prior*, reflecting the a priori probability of those causes[13] [$P(s)$]. Consequently, as highlighted by Friston (2010), perception can be understood as the process of inversely using the likelihood model (mapping from causes to sensations) to access the *posterior* probability of the causes, given the available sensory data (mapping from sensations to causes). In practice, during a given trial, a Bayesian model effectively approximates the posterior beliefs of decision-makers regarding the underlying causes or states (s) that give rise to the observed input or observation (x).

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[13] Also called in the literature hypotheses or states (s)

This approximation is achieved through the utilisation of Bayes' theorem:

$$P(s|x) \propto P(x|s) \, P(s)$$

Hence, Bayes' rule provides a formal framework for the decision maker exposed to a specific set of observations, to allocate probabilities (representing degrees of belief) to presumed states of the world. In essence, the brain makes use of prior beliefs and combines them with sensory evidence to form posterior probabilities. These posterior beliefs can be computed recursively over time using Bayes' theorem. This iterative process, commonly known as *Bayesian updating*, assumes that the observations (x_t) arrive sequentially over time. In the context of a standard RDM paradigm featuring two opposing directions of motion (for instance s_1 and s_2), and under the assumption of independent consecutive observations, the Bayesian updating equation takes the subsequent form (Bitzer et al., 2014):

$$p(s|X_{1:t}) \propto p(x_t|s) \, p(s|X_{1:t-1})$$

In this equation, the posterior belief over the s state is computed by weighting the likelihood of observation x_t under alternative s with the previous posterior belief $p(s|X_{1:t-1})$. Thus, it represents the brain's updated beliefs after taking new sensory information into account.

Hence, it is postulated that the decision-maker endeavours to align its internal generative models with those of the input process, to optimise its responses. Indeed, events that align with our initial expectations can be predicted to optimise behaviour. On the other hand, events that deviate from our expectations are considered *surprising*, often resulting in behavioural costs (e.g., slower responses) and prompting an update of the internal model to enhance future predictions (Itti & Baldi, 2009).

The process of revising an internal model of the external world due to a surprising event finds expression in the amplitude of the Event-Related Potential (ERP) component called P3 (Kopp, 2008; Kopp et al., 2016, 2020; Visalli et al., 2021, 2023), predominantly attributed to signalling from the locus coeruleus (LC) and the noradrenergic (NA) pathways (Bland & Schaefer, 2012). Interestingly, some studies have tried to analyse surprise and updating as distinct phenomena. For instance, O'Reilly and colleagues (2013) utilised a task manipulation that enabled the isolation of a subset of surprising events that did not trigger updates. They observed that surprise was associated with the posterior parietal cortex, while the ACC was related to Bayesian updating. In contrast, divergent findings have situated the updating process within the frontoparietal network (FPN), as evidenced by studies conducted by Kobayashi & Hsu, (2017); Schwartenbeck et al., (2016) and Visalli et al., (2019). The alignment between Visalli's

temporal findings and earlier non-temporal research underscores the conclusion that the frontoparietal network (FPN) encodes updating, regardless of the type of information being updated. Moreover, in the study by Visalli et al. (2019), it was observed that the cingulo-opercular network (CON) exclusively correlated with surprise.

Yu & Dayan (2005) extensively examined a particular form of surprise: unexpected uncertainty. Indeed, these authors proposed an interesting division between *expected* and *unexpected* uncertainty[14]. The former arises from acknowledging the inherent unreliability of predictions within a familiar context. Acetylcholine (ACh) signalling is associated with this form of uncertainty. In contrast, *unexpected* uncertainty emerges when the environment undergoes significant changes that defy pre-established expectations. Noradrenaline (NA) might be linked to this sort of unexpected alteration. Specifically, the NA activity corresponding to unexpected uncertainty seems to manifest in a phasic manner, whereas prolonged unexpected uncertainty, like volatility, may be indicated by sustained or tonic levels of NA activity, rather than these brief phasic bursts (for an in-depth exploration of the various facets of uncertainty refer to Bland & Schaefer, 2012). The degree to which a surprising event induces a change in beliefs is determined by different factors, including the volatility of the environment (Behrens et al., 2007; Nassar et al., 2010) and the precision of our existing beliefs (confidence) (Courville et al., 2006; Meyniel, 2020). This kind of confidence is of paramount importance for discerning when updates to our environmental model are warranted and when they are not. For example, when dealing with sporadic train delays, it is prudent to avoid making the unrealistic assumption that trains are consistently late (Meyniel, 2020). Interestingly, Meyniel's study illustrated how confidence in predictions affects beta-range (15–30 Hz) EEG oscillations and pupil-linked arousal, specifically tonic pupil size.

Thus far, I have elucidated three primary models that have been utilised for the examination and analysis of decision-making behaviours and correlated neural activity: the Drift-Diffusion, Predictive Coding, and Bayesian Models. Predictive coding stands as the initial framework that accentuates the inherent predictive nature of the brain, as well as its iterative procedure for minimising predictive errors. On the other hand, Bayesian models underscore the brain's aptitude for integrating pre-existing beliefs with sensory data to employ adaptive behaviours. In contrast, the drift-diffusion model concentrates on the dynamics of evidence accumulation only through a bottom-up process. The crucial advantage of the Bayesian model over the other

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[14] To see the difference between informational uncertainty from expected uncertainty and the similarities between environmental uncertainty and unexpected uncertainty, see Mathys et al 2014.

two is its foundation in an accurate delineation of the inner models of how sensory input is formed, accommodating prior beliefs. Notably, Bayesian models organically encompass the observer's perceptual uncertainty as a fundamental parameter for explicating behavioural patterns. Furthermore, Predictive coding and Bayesian inference share a common understanding of the significance of integrating sensory input with predictions. However, they differ in the type of data they utilise. Bayesian models excel in mathematically computing predictions, whereas predictive coding is more focused on neural mechanisms and representations, particularly hierarchical interactions between forward and feedback signals driving information processing and learning. To fully harness the strengths of these frameworks, we may have to await further insights from the Free Energy Principle (FEP). Indeed, hierarchical predictive coding approaches, which were initially developed in the domain of perception, have recently been extended by Friston and others to include action (i.e., policy selection) and to propose a unifying theory explaining how the brain works (Friston, 2009, 2010). If this unifying model is accurate, perception and action are inextricably linked and work together to reduce prediction error by shaping and selecting sensory inputs.

1.2.3 The Free Energy Principle

The Free Energy Principle (FEP; Friston et al., 2009; Friston, 2010), is a unifying theory that promises to bring perception, cognition, attention and action together within a common framework. Friston and his colleagues hypothesised that perception and action mechanisms share similarities; however, the key distinction is that motor error signals are not cancelled out by neuron mediating mechanisms (see Predictive coding). Instead, this cancellation occurs through the interaction of the organism with the environment, leading to changes in sensory input and proprioceptive information.

Formally, FEP is a mathematical description of how adaptive systems (i.e., biological agents) resist a natural tendency towards disorder, and thus how they maintain their states and structure in a constantly dynamic environment (both internal and external; Friston, 2010). It is crucial to highlight that this framework is not referring only to brains and individuals but, as Friston and colleagues (2023) recently have affirmed, "FEP allows one to simulate and predict the sentient behaviour of a particle, person, artefact or agent".

The reasoning is that excellent expected world models help us maintain our structure and organisation, and the better the fit between what we predict and what actually is, the smaller

the *free energy*. In the realm of reinforcement learning (RL) and optimal decision theory, learning was traditionally believed to revolve around minimising prediction error (Friston, 2010). As a result, many computational frameworks derived from these theories view the brain's role as an optimization process aimed at minimising certain functions. Notably, Friston and colleagues introduced the concept of free energy, suggesting that all these quantities can be viewed as essentially the same, and under certain simplifying assumptions, free energy can be equated with prediction error (Friston, 2009).

According to FEP, the long-term need to preserve physiological conditions translates into the short-term avoidance of *surprise*. A general brain function is thus to update prior beliefs to build accurate predictive models that minimise surprise between recently acquired information and prior beliefs. In this sense, surprise can be defined as the computed improbability of a sensory condition given an environment model (more formally, it is the negative log probability of an outcome; Clark, 2013; Friston, 2009, 2010). To avoid it, biological agents can assess their free energy, which is a function of two variables that the agent has access to (1) its sensory states and (2) the probabilistic representation of what caused a particular sensation (*recognition density*) encoded by its internal states (for example, neuronal activity; Friston, 2009, 2010). Thus, agents that minimise free energy also minimise surprise (Friston, 2010), since better models of the world make better predictions. In statistical terminology, free energy minimization is a sort of approximation of Bayesian inference in which model parameters are modified to maximise prediction accuracy starting with a generative model inferred by the biological system structure.

A corollary of the free energy principle, namely the *active inference*, explains better the relationship between perception and action. Following this perspective, the minimization of the free energy may be accomplished in two ways: the brain could optimise the internal generative models through inference and learning, or it can act on the environment to change the sensory input so that it is more compatible with the predicted model (Friston et al., 2017; Parr & Friston, 2019). This requires the existence of a shared objective function (*variational free energy*) for action and perception that evaluates the fit between an internal model and reality (Parr & Friston, 2019).

In the past years, a multitude of computational models has endeavoured to approximate subjects' beliefs from their observable decisions. Yet, this pursuit encountered challenges due to the so-called *Inverse Bayesian Decision Theory (IBDT) dilemma*: the updating of Bayesian

beliefs necessitates the computation of intricate integrals thus becoming analytically complex (Daunizeau et al., 2010). However, recent theoretical breakthroughs have illuminated a path forward by enabling computationally efficient approximations of exact Bayesian inference during learning (Daunizeau et al., 2010; Friston, 2009; Friston et al., 2023; Mathys et al., 2011, 2014). These advances represent a specific instantiation within the broader Bayesian brain hypothesis, potentially manifesting also as an application of the Free Energy Principle.

1.3   Bayesian modelling of decision-making and volatility

Over the past two decades, the boundary between neuroscience and computational models has become increasingly blurred. The integration of computational models into neuroscience is crucial, serving to rigorously test alternative hypotheses and yield novel predictions (Griffiths et al., 2012). Importantly, to achieve this, it is important to employ models that go beyond simple curve-fitting and truly capture the complexity of the data. Computational models offer a notable advantage in that sense because they allow for the optimization of unknown parameters within a model based on observed behaviour and experimental events. This optimization process enables the exploration of latent variables that play a role in mediating performance.

As previously mentioned, Bayesian algorithms have been harnessed for the modelling of decision-making processes (Behrens et al., 2007; Mathys et al., 2011; Nassar et al., 2010). To provide a concrete example, Bitzer et al. (2014) leveraged the perceptual decision-making dataset from Philiastides et al. (2011), encompassing accuracy and reaction time measurements. This dataset was employed to estimate the parameters of a Bayesian model. The authors also have modelled the process of how noisy sensory evidence is accumulated within a single trial (indeed, participants were required to distinguish between noisy stimuli depicting faces or cars). Nevertheless, in real-world scenarios, certain stimuli hold a higher probability of being observed than others. Hence, it becomes imperative to incorporate and model these types of variables and the predictive mechanisms involved. For instance, the perceived direction of motion in a RDK task often displays biases influenced by implicit predictions drawn from previous trial experiences. This is an area where Bayesian models can potentially shine, as they can elegantly integrate such direction probabilities into their framework. While Bitzer et al.'s study was deficient in manipulating stimulus occurrence probabilities, the work by Behrens et al. (2007) did involve the manipulation of probabilities. This work was of

paramount importance for the emergence of the *volatility* concept within decision-making experiments. Behrens et al. (2007) highlighted that learning processes are also determined by the estimated environmental volatility. Volatility is defined as a change in the frequency of existing circumstances over time (Behrens et al., 2007; Bland & Schaefer, 2012). Intriguing insights propose that humans navigate a volatile decision-making environment through the application of Bayesian principles (Behrens et al., 2007; Nassar et al., 2010). Updates to our estimations of environmental volatility are directly related to prediction errors regarding stimulus probabilities. Likewise, our estimations of stimulus probabilities are adjusted based on prediction errors associated with actual stimulus occurrences. Notably, Behrens et al. (2007) revealed that employing an ideal Bayesian model empowers human participants to optimally assess volatility leading to adaptive adjustments in value-based decision-making strategies. The task administered was a one-armed bandit task where participants were required to choose between blue and green stimuli. Participants must repeatedly choose between these options over multiple trials to maximise their cumulative rewards. The task encompassed trials featuring a stable 75% probability of a blue stimulus as the winning option, as well as trials where reward probabilities alternated between 80% blue and 80% green every 30 or 40 trials, constituting an unstable and volatile condition. The hypothesis was that the optimal agent is the one who makes the best use of previous data to track reward probabilities, calculating the value of each new piece of information they receive. Moreover, after a surprising event, the observer may allocate greater significance to unexpected information to recalibrate their expectations and decisions (Wilson et al., 2010). A sequence of unexpected events raises estimated volatility, and hence the learning rate (Behrens et al., 2007). Behrens' study exemplified the crucial understanding that achieving optimal decisions goes beyond mere integration of recent reward outcomes into a single action-outcome association. Instead, it necessitates a continuous monitoring of the environmental statistics to gauge the significance of each incoming piece of information. It is important to note, however, that while this model addressed value-based decision-making processes, it conspicuously lacked the manipulation of probability in the context of perceptual decision-making. Indeed, the overarching aim of the present thesis was to furnish empirical validation regarding how probabilities exert influence on behaviour within the realm of perceptual decision-making.

2 Aims and Hypotheses

The primary objective of this study was to investigate how predictions concerning probabilistic contexts influence perceptual decision-making in a motion detection task. Our research seeks to augment the existing body of knowledge in several critical ways.

Firstly, while prior research on perceptual decision-making has primarily concentrated on how sensory information guides behaviour — often by exclusively modelling sensory uncertainty (e.g., Bitzer et al., 2014) — and has employed models that assume a bottom-up processing approach and straightforward accumulation of evidence (e.g., drift-diffusion models), our inquiry delves into how top-down predictions impact participants' performance in a volatile environment. Secondly, we employ a Bayesian computational model, which confers a unique advantage by allowing us to operationalize predictions about left and right dot motion in each trial based on past information. The resulting variable was harnessed to examine the effect of predictions regarding the most probable motion on behaviour. The model used was the Hierarchical Gaussian filter model (Mathys et al., 2011), which allowed us to generate an Ideal Bayesian Observer.

Aligned with the Free Energy Principle (FEP) and the broader Bayesian Brain framework, our hypothesis posits that a fundamental cognitive function involves continually updating prior beliefs to construct precise predictive models while minimising the disparity between new information and existing beliefs. To this end, our experimental design places considerable emphasis on predictive processing, scrutinising how perceived motion direction can be biased due to an implicit prediction of the most probable direction, rooted in previous trial experiences. Indeed, our study employs a novel version of the random dot motion (RDM) task known as the *probabilistic* Random Dot Kinematogram (pRDK). This task introduces volatility by manipulating the probability of observing rightward motion throughout the task. We postulate that when evidence skewed in one direction is presented, participants expect to encounter trials in the most frequent direction, leading to enhanced performance. Consequently, according to our experimental hypothesis, participants will demonstrate shorter RTs when the presented stimulus aligns with their expectations. Conversely, a performance decline is expected when there is an incongruence between the predictions and the observed stimulus. Furthermore, we hypothesise that observers will predominantly rely on prior expectations when they are reliable, particularly in scenarios of ambiguous stimuli (i.e., low coherence levels).

3 Methods

This thesis encompasses two studies: Experiment 1 and Experiment 2 (pilot study). While rooted in a similar design framework, these two endeavours exhibit nuanced variations.

3.1 Experiment 1

The primary purpose of the first experiment was to determine whether predictions about motion direction impact participants' behaviours within an RDK task. Therefore, the effect of probabilistic manipulation on the RTs of participants was explored. To control motion direction predictions, the percentage of trials displaying RDK with a rightward direction varies throughout the task. Furthermore, we utilise an adaptive procedure to ensure that all participants perceive the global dot motion, hence ensuring participant learning of the direction probabilities (further elaborated upon in the Adaptive procedure section). This study involved a computerised task and took place in a controlled laboratory setting.

Participants

The final participant sample comprised 41 adults [25 females; mean age: 21,76 years (standard deviation, SD = 1,51), range: 20–26 years]. All of them were assessed with the Edinburgh Handedness Inventory (Oldfield, 1971) [mean: 78.21; standard deviation, SD = 27.49]. They all reported having a normal or corrected-to-normal visual acuity, being in good health and with no history of neurological or psychiatric illness. The procedures involved in this study were approved by the Local ethical committee. Moreover, participants gave their written informed consent before the experiment, in accordance with the Declaration of Helsinki (World Medical Association, 2013).

Procedure

Once arrived at the laboratory, participants were asked to provide personal information (name, age, sex and level of instruction), complete a questionnaire on hand dominance (the Edinburgh Handedness Inventory; Oldfield, 1971), and confirm the absence of any neurological or psychiatric diagnoses as well as the absence of any pharmacological treatments that could compromise cognitive functioning within the past 5 years. Furthermore, they were asked to sign the informed consent, where they were provided with information about the study and its requirements. Subsequently, they were taken to a soundproofed environment and positioned at

57 cm from a 52 x 29 cm monitor with a 60 Hz refresh rate and 1080x220 resolution. The experiment started with the presentation of instructions which comprise examples of the stimuli as well. The instructions were displayed within various frames and read as follows: "*Stai per eseguire un compito di percezione del movimento. Ad ogni prova vedrai dei puntini che si muovono al centro dello schermo. Una parte di essi si muoverà coerentemente verso destra o verso sinistra. Gli altri si muoveranno in direzione tutte diverse e casuali. Il tuo compito è semplice: premi F se ti sembra di percepire un movimento verso sinistra; premi J se ti sembra di percepire un movimento verso destra. Posiziona le mani sulla tastiera mettendo l'indice destro sul tasto J e l'indice sinistro sul tasto F. Cerca di rispondere il più velocemente possibile e cercando di non commettere errori. Non c'è pratica. Se è tutto chiaro premi la barra per iniziare*"; [English version: "You are about to perform a motion perception task. In each trial, you will see dots moving in the centre of the screen. Some of them will move coherently to the right, and others will move in various random directions. Your task is simple: press 'F' if you perceive motion to the left and 'J' if you perceive motion to the right. Place your hands on the keyboard with your right index finger on the 'J' key and your left index finger on the 'F' key. Try to respond as quickly as possible while minimizing errors. There is no practice session. If everything is clear, press the spacebar to begin"]. During the experiment, participants' responses were recorded.

Experimental Design

The experimental paradigm was implemented in MATLAB (The MathWorks, Inc., Natick, Massachusetts, United States) using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Each trial featured a centrally presented RDK stimulus comprising 600 moving dots. Examples of RDKs with different coherence levels are visually depicted in Figure 8.

On each trial, participants had to respond as quickly as possible to the leftward/rightward direction of dots moving coherently within background noise (dots moving with random directions). Participants responded by pressing the "F" key with their index finger if they saw a left direction and the "J" key if they saw a right direction. No feedback was provided in case of an erroneous response. A trial started with the presentation of a red fixation spot for 500 ms followed by 600 moving dots lasting 100 ms and the response time was 1500 ms after the offset of the stimulus (this experimental design is illustrated in Fig. 9). Because of the short duration of the stimulus, information must be integrated almost instantly. As a result, it avoids

introducing persistent noise (i.e., temporal noise) into the decision-making system, which has been observed in longer Random Dot Kinematograms (RDKs) as demonstrated by Genest et al., 2016.
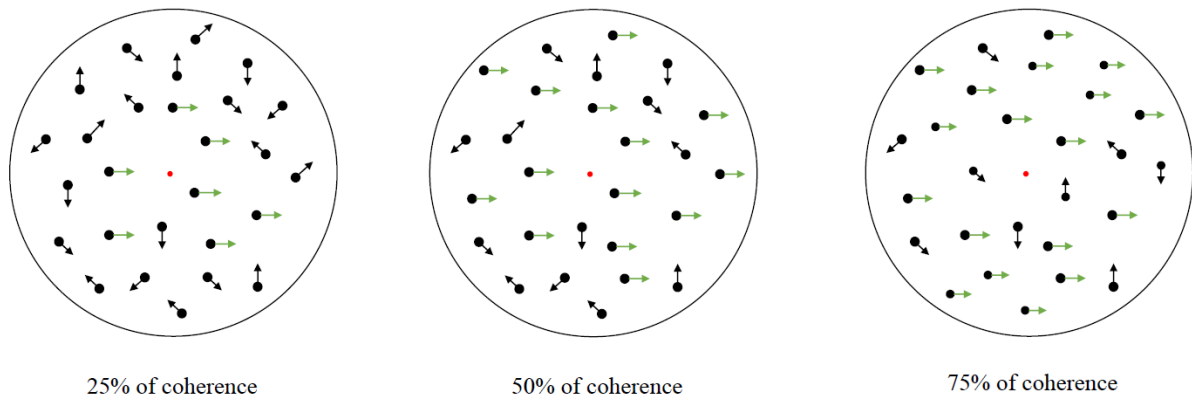

25% of coherence   50% of coherence   75% of coherence

Figure 8 | Example of RDKs with different levels of coherence (25%; 50%; 75%). A percentage of dots move coherently in the same direction (indicated by the green arrows), while the remaining dots move in random directions. Note that these levels of coherence were not fixed in this experiment (see text for more details).
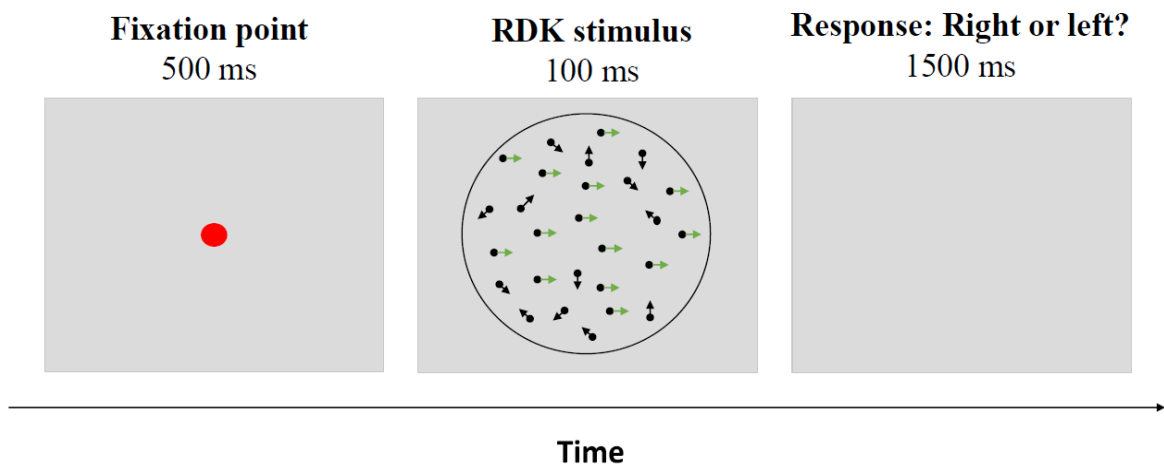

Fixation point
500 ms

RDK stimulus
100 ms

Response: Right or left?
1500 ms

Time

Figure 9 | Experimental design experiment 1. Each trial started with the presentation of a fixation spot followed by 600 RDK dots that moved in the centre of the screen. A part of them moved consistently to the right or the left. The others moved in different and random directions (random dots). The task was to press F if a movement to the left was perceived and to press J if a movement to the right was perceived.

Since we aimed to test the effect of probabilistic contexts on behaviour, we used a novel paradigm known as pRDK. To control the prior expectations on motion direction, we used a block design: the probability of perceiving rightward motion was manipulated so that the probability of observing it changed over time. The trials were grouped into 12 experimental

blocks and 4 runs. Each run included three experimental blocks with varying probabilities of right movement [P(right)]: 0.2, 0.5, and 0.8, which corresponded to the relative frequency of the specific direction (left or right) within each experimental block.

$P(right) = 0.2$. The 0.2 refers to the block in which the proportion of trials presenting RDK with a rightward movement is 20% while the percentage of trials with leftward motion is 80%.

$P(right) = 0.5$. The number of trials presenting an RDK with the coherent movement to the right or left is the same (50%-50%).

$P(right) = 0.8$. Finally, the experimental trials with the right probability set at 0.8 relate to the presentation of RDK trials with the right direction of movement being 80% and the probability of presentation of RDK trials with the left direction of movement being 20%.

It is worth noting that the participants were not aware of the varying degrees of rightwards probability, and information about the starts and endings of the various experimental blocks was not provided. In conclusion, by presenting participants with a scenario in which one event noticeably outweighs its opposite counterpart (observed under the conditions P(Right)=0.2 and P(Right)=0.8), we expected to induce an anticipatory expectation that the more frequent event would persist in future trials.

Because the computational parameters of the learning process are dependent on the precise ordering of trials (Vossel et al., 2015), we decided to present each subject with the same sequence of trials, as typical of other computational research of trial-by-trial learning (e.g., Behrens et al., 2007; Iglesias et al., 2013). This guarantees that changes in model parameters may be ascribed to subject-specific rather than task-specific aspects.

This experiment was divided into two phases: the *adaptive phase*, and a subsequent testing phase (*experimental phase)*. The total duration of the experiment was about 40 minutes marked by 5 fixed pauses each of 30 seconds signalled by a countdown. The first break was positioned at the end of the adaptive phase, while the subsequent pauses punctuated four distinct runs of the experimental phase.

Adaptive phase

After instructions, 200 trials of a *Psychophysical Bayesian adaptive procedure* were presented with the sampling of different coherence levels and the right direction probability set at 50% (hence, half of the trials showed a left motion and the other half a right motion). No training was presented before the beginning of the task because the first trials were used for this adaptive procedure. Specifically, we used Luigi Acerbi's MATLAB implementation of the PSI method (https://github.com/lacerbi/psybayes) by Kontsevich and Tyler (1999), extended to include the lapse rate (Prins, 2012). This method allows for the acquisition of both the sensitivity threshold and slope of the psychometric function for each subject. As a result, estimated accuracy values are obtained for each coherence value. If the accuracy value at 100% coherence falls below 90% on the plotted psychometric curve, this phase is deemed unsuccessful. Failure to pass the adaptive phase led to the termination of the experiment.

In essence, the purpose of this phase was to "standardise" the task's difficulty level for all participants and ensure that all individuals perceive the global movements presented in the subsequent phase.

Experimental Phase

After the adaptive phase, 400 experimental trials were presented. The trials were grouped into 12 experimental blocks and 4 runs. Between one run and the next one, there were fixed pauses of 30 seconds each, and every run contained 3 experimental blocks with varying right movement probabilities: 0.2, 0.5, and 0.8.

In terms of the coherence that characterises the RDKs, only one level of coherence was chosen in this phase based on the coherence that allowed for 90% accuracy in the adaptive phase. This makes it possible to have a stimulus with little sensory uncertainty. Thus, during the experimental phase, the level of coherence remains constant while the probability of motion direction changes.

3.2 Experiment 2 (Pilot study)

This experiment served as a preliminary investigation preceding a forthcoming main study, which will combine high-density electroencephalography (hd-EEG) with eye tracking and pupillometry. The objective extended beyond testing the influence of probability context on

behaviour; it also included the first steps towards understanding the intricate interaction between coherence levels and the predictions of rightward\leftwards occurrence. It involved a computerised task and took place in a controlled laboratory setting.

Participants

The final participant sample consisted of 18 adults [13 females; mean age: 21.6 years (standard deviation, SD = 2.3), range: 19–26 years]. All participants attested to possessing normal or corrected-to-normal visual acuity, maintaining good overall health, and lacking any history of neurological or psychiatric conditions. The research procedures undertaken in this study were granted ethical approval by the Local Ethical Committee. In alignment with the principles outlined in the Declaration of Helsinki (World Medical Association, 2013), participants provided written informed consent before they participated in the experiment.

Procedure

The participants arrived in the laboratory and were asked to provide personal information (name, age, sex and level of instruction). They all confirmed the absence of any neurological or psychiatric diagnoses as well as the absence of any pharmacological treatments that could compromise cognitive functioning within the past 5 years. Furthermore, they were asked to sign the informed consent. Subsequently, they were taken to a soundproofed environment and positioned at 64 cm from a 52 x 29 cm monitor with a 60 Hz refresh rate and 1080x220 resolution. Participants' heads were stabilised using a chin and forehead rest. To comprehensively capture gaze data and pupillometry, a video-based eye tracker was employed. It is noteworthy that an ongoing analysis of this dataset is currently underway. The instructions mirrored those from experiment 1, inclusive of illustrative examples of the stimuli. During the experiment, participants' responses were recorded. After completing the study, their impressions and feedback about it were collected in a debriefing phase, and participants were asked if they had noticed that the probability direction varied during the task.

Experimental Design

The experimental paradigm was implemented in MATLAB (The MathWorks, Inc., Natick, Massachusetts, United States) using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

Analogous to Experiment 1, a probabilistic Random Dot Kinematogram (pRDK) task was administered, and we used a block design to control the prior expectations on motion direction. The probability of rightward motion was meticulously partitioned into three discrete levels: 0.25, 0.5, and 0.75. In contrast with experiment 1, here the task solely encompassed the experimental phase due to its pilot nature, which aimed to evaluate the eye-tracker recording process and the interaction between direction probability and motion coherence. Consequently, the RDK stimuli were configured to exhibit three discrete coherence levels: 15%, 25%, and 100%. Precisely, half of the trials (50%) featured stimuli with complete coherence (100%), while a quarter (25%) showcased stimuli with a coherence level of 25%. The remaining 25% of trials were designed with a coherence level of 15%. Thus, this comprehensive design facilitated a nuanced exploration of the impact of coherence level as well as context probability on behaviour.

On each trial, participants had to respond as quickly as possible to the leftward/rightward direction of dots moving coherently within background noise (dots moving with random directions). Participants responded by pressing the "F" key with their index finger if they saw a left direction and the "J" key if they saw a right direction. No feedback was provided in case of an erroneous response.
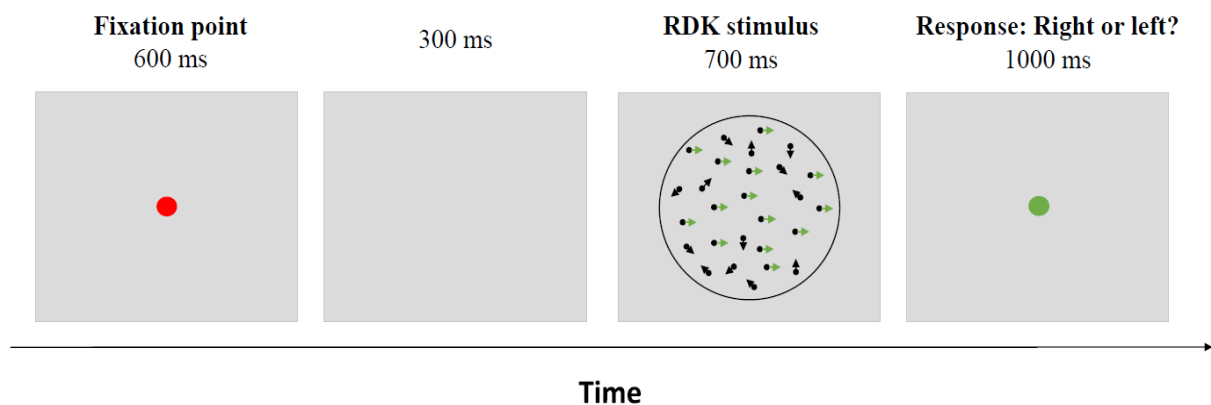

Figure 10 | Experimental design experiment 2. Each trial started with the presentation of a fixation point followed by 600 RDK dots that moved in the centre of the screen. Among these dots, a portion exhibited consistent movement to the right or left, while the remainder moved in diverse and random directions, constituting the random dots. Participants were tasked with the assignment of pressing the 'F' key when perceiving leftward movement and the 'J' key for rightward movement. Notably, responses could be provided even during the ongoing stimulus presentation. To avoid eye-tracking bad data, a green fixation point was introduced, encouraging participants to attempt blinking during this specific interval and not before.

The sequence of task events unfolded in the following manner (shown in Fig. 10): an initial fixation screen persisted for a duration of 600 ms, succeeded by a fixation-absent screen lasting 300 ms. Subsequently, the Random Dot Kinematogram (RDK) stimulus appeared and persisted for 700 ms. Participants had the flexibility to initiate their response either during the RDK stimulus presentation or subsequently, with a time window of 1000 ms remaining for the response after the offset of the stimulus. It is noteworthy that an extension in the stimulus duration was implemented compared to Experiment 1, which was needed to facilitate the capture of saccadic movements during eye-tracking recording.

3.3   Data Analysis

The analysis aimed to test the effect of the probability of the rightward direction (specifically, the Bayesian rightwards probability; prx) on the participant's behaviour and the interaction between the probability of motion direction and coherence levels. To analyse the RT data, a linear mixed model (fitted by minimising the Restricted Maximum Likelihood criterion; REML) was chosen because it allows the investigation of the relationship between trial-wise direction probability and response speed while considering the variability in mean performance among participants through random effects and controlling for confounders. Crucially, LMM provides the opportunity to analyse data from repeated measures as well as incorporate sequential dependencies into the model's definition. Additionally, they might yield a slight enhancement in statistical power and provide improved safeguards against Type II errors (Baayen & Milin, 2010). The analysis was implemented in R Statistical Software (v4.1.2; R Core Team 2021) using the lme4 package (Bates et al. 2022).

Model-based measure of predictions using an Ideal Bayesian Observer

To operationalize the predictions of the left and right dot motion in each trial based on previous information, an Ideal Bayesian Observer was used. The resulting measure was called Bayesian rightwards probability (*prx*) which will be then utilised in the data analysis to test the effect of predictions on behaviour. This variable was created using the MATLAB Hierarchical Gaussian Filter (HGF) toolbox (Mathys et al., 2011, 2014), open-source code available as part of the TAPAS software collection (Frässle et al., 2021). A theoretical framework of this method is presented in Figure 11. This toolbox allows predicting the value of a hidden and moving variable based on the information gathered up to that moment. Indeed, it is unlikely that the brain processes directional motion probabilities discretely at the block level, where the initial

trial within a block directly corresponds to the overall rightwards probability of the entire block. A more plausible hypothesis is that the brain develops its expectations for future events gradually and on a trial-by-trial basis, as depicted by the continuous black line in Figure 12.
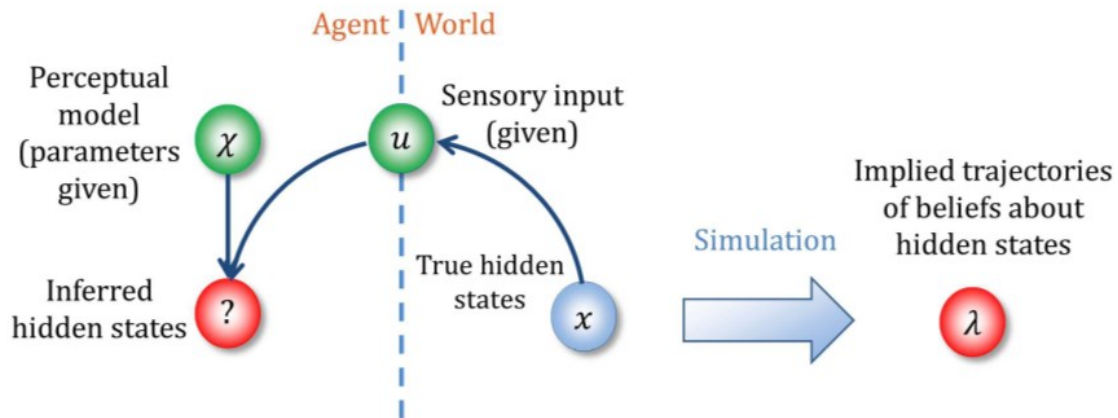

Figure 11 | Operating within a well-defined framework, the toolbox (Frässle et al., 2021) facilitates the formalisation of interactions between an agent and its environment. This dynamic involves the agent receiving a sequential stream of inputs (u). These inputs are pivotal in the process of deducing concealed states of the world, encapsulated as beliefs (λ). This inference procedure is rooted in the utilisation of a perceptual model, parameterized by χ. The outcome of this modelling effort is an estimated set of perceptual parameters, which in turn enables the generation of simulated trajectories tracing the evolution of beliefs about hidden external states (illustrated in Fig. 11) trial-by-trial.
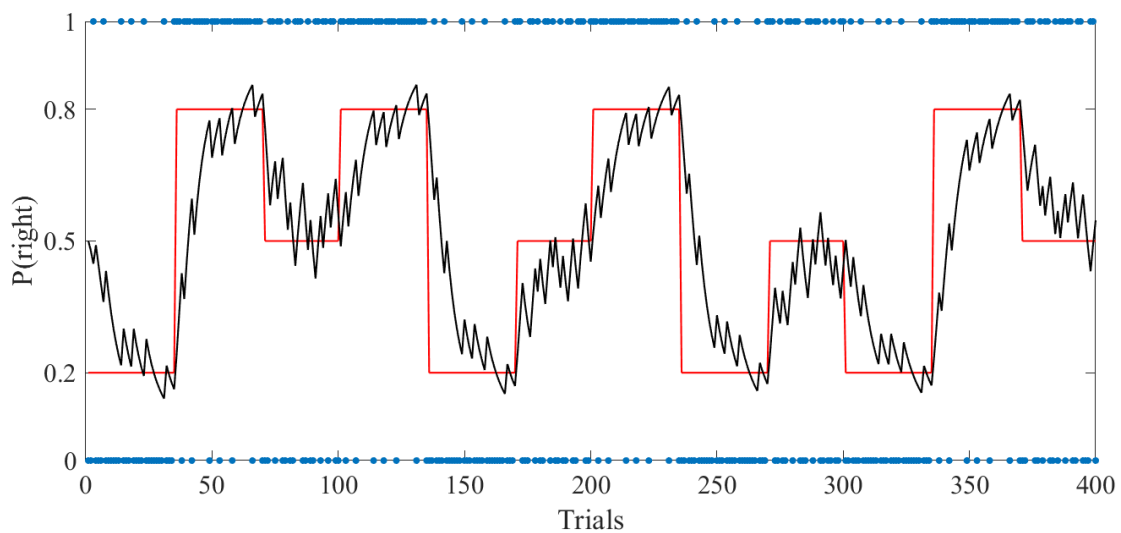

Figure 12 | Based on the input, the HGF toolbox infers the agents' beliefs (posterior probabilities) about the probability that the next outcome will be 1 (right motion) or 0 (left motion). *Black*: posterior probability of the input u=1; $\hat{\mu}$, (trial-wise rightwards probability). *Red*: the block-wise manipulated probability of the input (right direction probability). *Blue*: sensory input (μ) of motion direction (0 refers to left direction and 1 refers to right direction).

Central to this toolbox's functioning is the HGF, a concept rooted in the works of Mathys et al. (2011) and (2014), which employs variational Bayesian techniques to update the probability of an event (in this case, the right motion) on each trial. This toolbox introduced a methodological avenue for fitting time series models through the lens of Bayesian inference. To describe a continuous uncertain quantity (such as the probability of occurrence of a rightwards or leftwards motion), this model uses Gaussian random walks. In essence, it computes two primary parameters, which are the learning rate and a measurement of environmental volatility. The volatility parameter grows if the probability of an input occurrence varies, hence it is determined by the probability of direction transitions. The term volatility dates back to Behrens et al. (2007) and in Mathys et al. (2011) it is defined as the variance of a time series per unit of time. For a more comprehensive explanation of how this model specifically works, see Mathys et al., (2011) and (2014) papers, as well as its applications, such as those illustrated by Iglesias et al. (2013), Visalli et al. (2023) and Voss et al. (2013).

Using the toolbox, we discerned the perceptual parameters that yield the minimal cumulative surprise for the given input sequence (i.e., the sequence of presented movement directions which is the same for each subject). Thus, the ideal observer minimises the surprise, namely, the prediction errors. The process of parameter estimation was executed via the *fitModel* function, thoughtfully configured with the following arguments:

- An empty array representing observed responses (i.e., []). Since we are only interested in constructing an Ideal Bayesian model, the specification of observed responses is unnecessary (cf. Mathys et al., 2014 to see other applications).
- List of movement directions presented to the subjects in the experimental phase as input u
- The type of perceptual model was the *binary enhanced Hierarchical Gaussian Filter* (eHGF).
- *Bayes_optimal_binary*, which gauges the surprise generated by new inputs based on the prevailing perceptual state.
- The *quasi-newton* optimization algorithm, a variant of the Broyden-Fletcher-Goldfarb-Shanno (BFGS) algorithm. This algorithm is harnessed to ascertain maximum-a-posteriori (MAP) parameter estimates.

By inverting the model from sensory inputs (i.e., the trial list of motion directions) alone we obtain trajectories and parameters which represent an ideal Bayesian agent, where "ideal"

means experiencing the least surprise about sensory inputs. The visualization of the simulated state/beliefs trajectory (posterior probability) of the ideal observer is shown in Fig. 12.

The resulting variable (i.e., the Bayesian right probability, more technically the posterior probability of the input u=1; $\hat{\mu}$) follows both Bernoulli and binomial distributions. In essence, the Bernoulli distribution is characterised by a mean and a variance which is intricately linked to the mean (Mathys et al., 2011). This variance assumes a bell-shaped curve, where increased variance corresponds to diminished predictive precision. Notably, when variance is high, it is associated with a situation of uncertainty (0.5 probability of right motion), while a stronger inclination towards either event 0 or 1 enhances predictive accuracy, manifesting as reduced variability. This concept harmonises seamlessly with our experimental design.

3.3.1 Experiment 1

RTs were transformed into inverse RTs (iRTs), that is, -1/RT, to mitigate the influence of non-normally distributed and skewed data. iRTs were then analysed using Linear Mixed Models (LMM). Data from error trials were not included. LMM analysis was conducted on RTs to test for the effect of the probabilistic direction conditions on RTs with the formula:

$$iRT \sim Run(z) * trial\,run(z) + preiRT + prx * direction + (prx * direction|id)$$

In detail, as fixed-effects terms, we entered as confounders the four runs ($Run(z)$), the order of trials ($trial\,run(z)$), and their interaction (specified by an asterisk), as well as the inverse RT at the preceding trial ($preiRT$). On the other hand, as effects of interest the right Bayesian probability (prx), the direction of the moving dots ($direction$) and their interaction were included. The random part of the model (specified between parentheses) included the by-subject random intercepts and correlated by-subject random slopes for the Bayesian probability (prx), the dots' movement direction ($direction$), and their interaction. All these continuous predictors were Z-scored to facilitate model convergence. Nonetheless, prx was excluded from z-scoring due to its computation based on the HGF ideal model. Prx already incorporates a sigmoid transformation, rendering it a continuous variable inherently centred around zero. While it might not conform to the SD=1 normalisation, the value of zero holds significance, representing the 0.5 (50%) right motion probability.

We included variables such as $trial\,run(z)$ and $preiRT$ in the model not only to avoid violating linear modelling assumptions of observation independence and to capture possible

effects of learning and fatigue but also to improve the fit as well as to bring temporal dependencies under control (Baayen & Milin, 2010).

3.3.2 Experiment 2 (Pilot study)

First, generalised linear mixed model (GLMM) analysis was conducted on accuracy, after a logit transformation, with the formula:

$$Accuracy \sim Run\ (z) * trial\ run(z) + Direction * Coherence * prx \\ + (Coherence + Direction * prx | ID)$$

As fixed-effects terms, we entered as confounders the runs ($Run\ (z)$), the order of trials ($trial\ run(z)$), and their interaction while as effects of interest the right Bayesian probability (prx), the direction of the moving dots ($Direction$), the z-scored level of coherence ($Coherence$) and their interaction was included. The random part of the model included the by-subject random intercept and correlated by-subject random slopes for the Bayesian probability, the dots' movement direction, and their interaction as well as the level of coherence ($Coherence$). The three-way interaction $Direction * Coherence * prx$ was excluded from the random component due to convergence issues with the model. Consequently, we simplified the model by removing this interaction. This decision was driven by the fact that the interpretability of prx depends exclusively on its interaction with motion direction, which led us to eliminate the interactions with the coherence. After removing this interaction, the model successfully converged.

Then, LMM analysis was conducted on RTs which were transformed into iRTs to mitigate the influence of non-normally distributed and skewed data. Data from error trials, trials with errors to the previous trial and anticipations were not included. This analysis was conducted with the formula:

$$iRT \sim Run(z) * trial\ run(z) + preiRT + Direction * Coherence * prx \\ + (Coherence + Direction * prx | ID)$$

In detail, as fixed-effects terms, we entered as confounders the runs ($Run(z)$), the order of trials ($trial\ run(z)$), and their interaction, as well as the inverse RT at the preceding trial ($preiRT$). On the other hand, as effects of interest the right Bayesian probability (prx), the direction of the moving dots ($Direction$), the z-scored level of coherence ($Coherence$) and their interaction was included. The random part of the model included the by-subject random intercepts and

correlated by-subject random slopes for the Bayesian probability, the dots' movement direction, and their interaction as well as the level of coherence ($Coherence$). The three-way interaction $Direction * Coherence * prx$ was not included in the random part for the same reason presented above in the GLMM. Also here, we included variables such as $Run\ (z)$ and $preiRT$ in the model to bring temporal dependencies under control (Baayen & Milin, 2010).

4 Results

4.1 Experiment 1

Trials with absolute standardised residuals greater than 2.5 SD were considered outliers and were deleted, as suggested by Baayen & Milin, 2010. After that, the model was re-fitted, and the key results are summarised in Table 1. Importantly, this analysis excludes error trials and the term [180] denotes leftward motion.

Table 1 | Experiment 1- Summary output of the final LMM model on iRTs.

Predictors	Estimates	CI	p
(Intercept)	-2.79	-2.92 – -2.65	**<.001**
Run (z)	-0.03	-0.4 – -0.02	**<.001**
Trial run (z)	0.02	0.01 – 0.03	**<.001**
PreiRTs	0.14	0.13 – 0.15	**<.001**
Prx	-0.10	-0.13 – -0.08	**<.001**
Direction [180]	0.04	-0.02 – 0.10	.217
Run (z)* trial run (z)	-0.01	-0.02 – 0.00	.274
Prx * Direction [180]	0.19	0.14 – 0.24	**<.001**

Marginal R^2 / Conditional R^2 0.057 / 0.467

Notes: Run refers to the z-scored run while Trial Run indicates the order of trials in each run. (z) refers to the predictors that were z-scored before analysis. PreiRTs refer to the inverse reaction times at the preceding trial. Prx refers to the Bayesian probability of right motion computed through HGF. [180] indicates left dot motion. The bold p-values indicate when statistical significance was reached.

The principal outcomes underscore the significant effect of the probability of rightward motion (prx) on $iRTs$. Moreover, a significant interaction materialises between the probability of rightward motion (prx) and the motion direction ($prx * direction$; this interaction is graphically depicted in Figure 13). In particular, when the direction was rightwards, individuals were faster if the probability of a rightwards direction was large ($prx = 1$). On the contrary, when the probability of such motion being to the right was low ($prx = -1$), the iRTs were prolonged. This pattern similarly holds when considering the leftward direction. This means that when the direction of motion and the high probability match, participants' responses are faster (i.e., shorter iRTs).
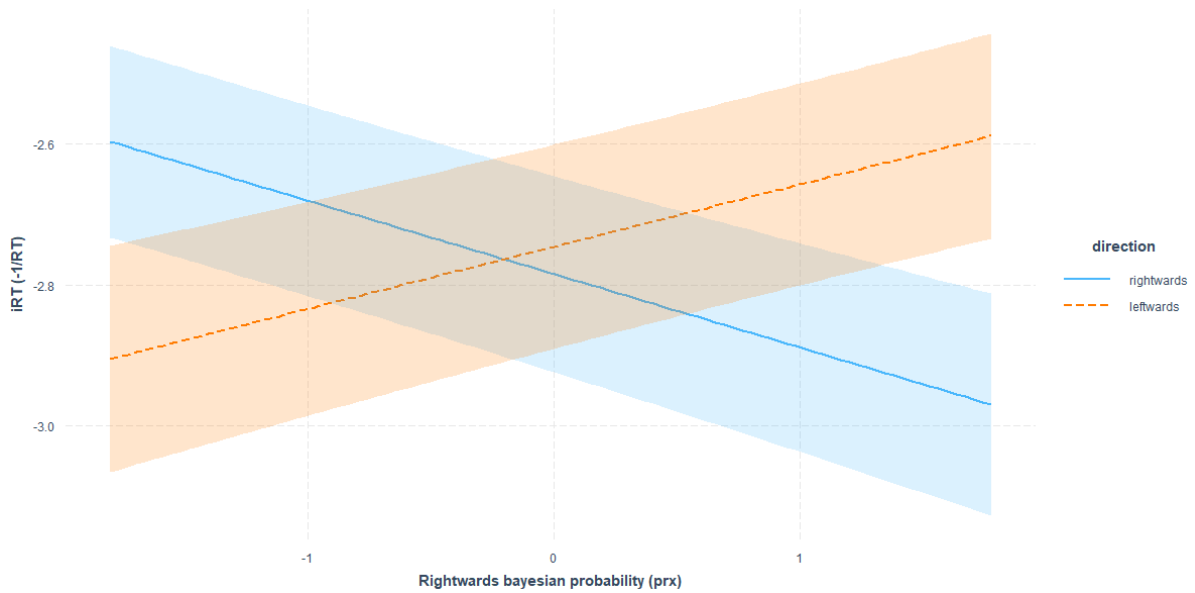
Figure 13 | Interaction effect between the direction and rightwards Bayesian probability (prx) on inverse RTs. The plot shows the conditional effect of Rightwards Bayesian probability (prx) on inverse RTs at the rightwards (blue line) and leftwards (orange line) direction of motion. Shaded error bars indicate confidence intervals.

4.2 Experiment 2 (Pilot study)

The pivotal findings concerning accuracy are succinctly outlined in Table 2.

Table 2 | Experiment 2 summary output of the final GLMM model on Accuracy.

Predictors	*Odds Ratio*	*CI*	*p*
(Intercept)	73.73	40.72 – 133.51	**<.001**
Run (z)	0.90	0.81 – 1.00	**.043**
Trial run (z)	1.00	0.91 – 1.11	.927
Direction	1.26	0.82 – 1.94	0.294
Coherence	3.71	2.20 – 6.26	**<.001**
Prx	1.00	0.78 – 1.27	.977
Run (z)* trial run (z)	0.88	0.80 – 0.98	**.015**
Direction*Coherence	1.02	0.75 – 1.39	.903
Direction * Prx	1.07	0.56 – 2.05	.844
Coherence * Prx	0.89	0.72 – 1.09	.249
(Direction*Coherence)*Prx	0.96	0.63 – 1.46	.841

Marginal R^2 / Conditional R^2 0.066 / 0.572

Notes: Run refers to the z-scored run while Trial Run indicates the order of trials in each run. (z) refers to the predictors that were z-scored before analysis. Coherence refers to the coherence level of the RDK. PreiRTs refer to the inverse reaction times at the preceding trial. Prx refers to the Bayesian probability of right motion computed through HGF. [180] indicates left dot motion. The bold p-values indicate when statistical significance is reached.

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As the trials unfold throughout a $Run\ (z)$, a noticeable trend emerges wherein accuracy diminishes, implying an increased occurrence of errors made by participants (negative association between the run and accuracy defined by an odds ratio less than 1). Furthermore, as expected, the greater the level of coherence, the higher the accuracy (significant effect of $Coherence$ on $Accuracy$). Finally, a significant interaction was found between Run and the order of trials ($Trial\ run\ (z)$). Notably, the probabilistic conditions (Prx), the direction of motion ($Direction$) and their interaction has no significant effect on accuracy.

Regarding the RT analysis, with the results summarised in Table 3, trials exhibiting absolute standardised residuals exceeding 2.5 standard deviations (SD) were identified as outliers and subsequently removed, as suggested by Baayen & Milin, 2010. After removing these outliers, the model was re-fitted.

Table 3 | Experiment 2 Summary output of the final LMM model on iRTs.

Predictors	Estimates	CI	p
(Intercept)	-1.21	-1.28 – -1.14	**<.001**
Run (z)	-0.02	-0.02 – -0.02	**<.001**
Trial run (z)	-0.00	-0.01 – -0.00	**.012**
PreiRT	0.02	0.02 – 0.02	**<.001**
Direction	-0.02	-0.04 – -0.00	**.014**
Coherence	-0.04	-0.05 – -0.04	**<.001**
Prx	-0.00	-0.01 – 0.00	.278
Run (z)* trial run (z)	0.00	0.00 – 0.01	**.010**
Direction*Coherence	-0.01	-0.01 – 0.00	**0.041**
Direction * Prx	-0.04	-0.06 – -0.02	**<.001**
Coherence * Prx	0.00	-0.00 – 0.01	.143
(Direction*Coherence)*Prx	-0.01	-0.02 – -0.01	**.001**

Marginal R^2 / Conditional R^2 0.066 / 0.572

Notes: Run refers to the z-scored run while Trial Run indicates the order of trials in each run. (z) refers to the predictors that were z-scored before analysis. Coherence refers to the coherence level of the RDK. PreiRTs refer to the inverse reaction times at the preceding trial. Prx refers to the Bayesian probability of right motion computed through HGF. [180] indicates left dot motion. The bold p-values indicate when statistical significance was reached.

Beyond the influence of control predictors on RTs, the findings revealed a noteworthy influence of both Direction and coherence levels ($Coherence$) on response speed. Specifically, there is a substantial impact of Direction, indicating a preference for responding more to one direction compared to the other. This bias is also visually evident in Figure 14. Additionally, interactions involving coherence ($Coherence$) and direction, as well as direction and

rightwards probability (*Prx*), exhibited a statistically significant effect on behaviour. Thus, participants exhibit quicker RTs to a right movement as the probability of a rightward motion increases (indicated by the dark blue line in Fig. 14). Furthermore, the sky-blue line illustrates a corresponding trend, wherein participants display enhanced speed in left responses as the probability of a leftward motion rises.
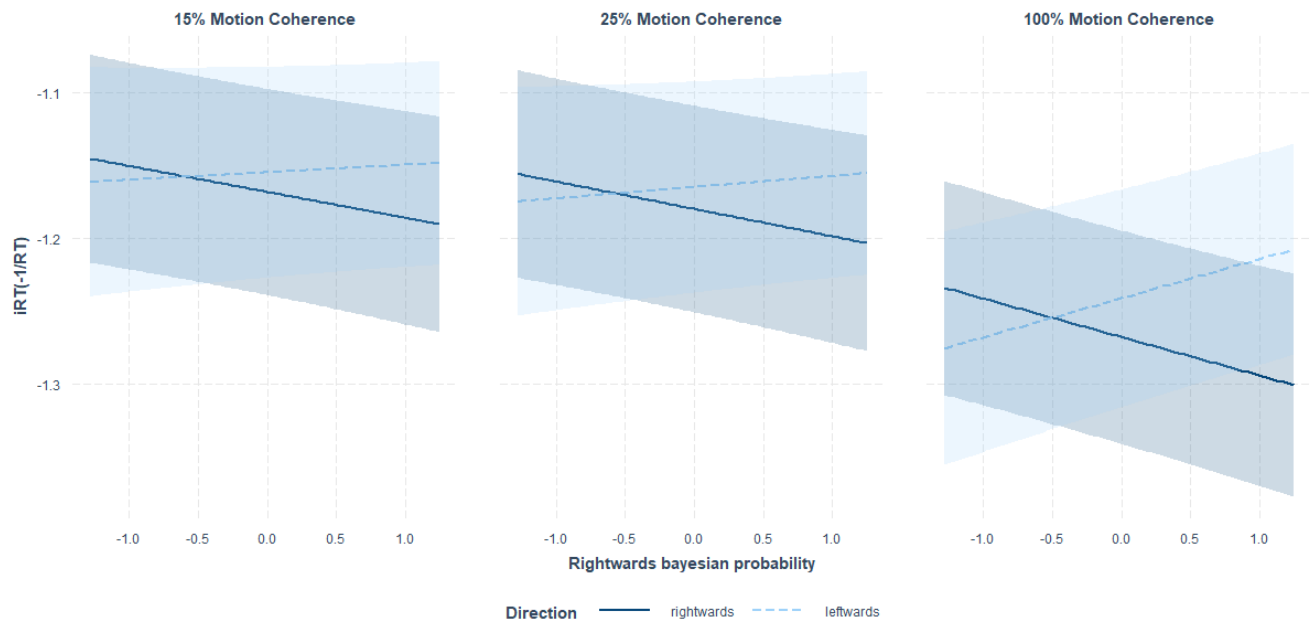

Figure 14 | Interaction plots of right bayesian probability (prx) and direction of motion (Direction) effects on inverse RTs at different coherence levels (15%; 25%; 100%). Participants exhibit quicker RT to a right movement as the probability of a rightward motion increases (indicated by the dark blue line). Furthermore, the sky-blue line illustrates a corresponding trend, wherein participants display enhanced speed in left responses as the probability of a leftward motion rises. Shaded error bars indicate confidence intervals.

5 Discussion

The current investigation delves into a pivotal aspect of how the probability of occurrence of events can be learned and subsequently impact perceptual decision-making performance. Although numerous studies predominantly manipulate sensory noise, it is crucial to consider that real-life scenarios involve stimuli with diverse occurrence probabilities that can be predicted to adjust our behaviour. In line with contemporary theories, the brain is now understood as a "predictive machine", engaging in optimal Bayesian inference rather than acting as a passive filter (Clark, 2013; Friston, 2005, 2009, 2010; Friston et al., 2017; Doya et al., 2006; Knill & Pouget, 2004). Given these insights, a comprehensive understanding of the computational processes underlying perceptual decision-making is needed, particularly focusing on the predictive mechanisms at work within dynamic experimental contexts (volatile environment). For instance, Behrens et al. (2007) manipulated reward probabilities to examine how volatility influences subjects' learning rates. Despite this progress, a gap remains in demonstrating the impact of volatile event probabilities on *perceptual* decision-making. Thus, in the current study, we deliberately manipulated the probability of stimulus presentation — specifically, the frequency of RDK stimuli directed towards the right or left. This manipulation skewed the prevalence of one direction within certain experimental blocks. Our goal was to explore the influence of these probabilities and the resulting volatility on the processes underlying perceptual decision-making. Through two experiments, we illustrated the role of top-down predictions in shaping behaviour: when subjects encountered a rightward motion and the probability of this happening was high, their response times decreased. Similarly, this pattern emerged for leftward motion when the probability of leftward movement was high. In essence, when predictions aligned with sensory evidence, responses were notably faster. This underscores the necessity of continuously monitoring environmental statistics to attain optimal decision-making behaviour.

Drawing from prior research that has effectively demonstrated the applicability of Bayesian inference in modelling information processing within uncertain contexts (Chater et al., 2010; de Lange et al., 2018; Friston et al., 2017), as well as in the context of volatility (Behrens et al., 2007), we employed a sophisticated approach to translate the discrete manipulated probability of rightwards motion into a continuous variable. Specifically, we leveraged a hierarchical Bayesian model, termed the Hierarchical Gaussian filter (Mathys et al., 2011), to operationalize an ideal Bayesian observer's prediction generating a trial-wise rightwards probability.

Given these considerations, I shall present the main results of the current studies in what follows.

In the first study, our focus was on examining the influence of probability on RTs. To achieve this, we intentionally maintained a low and consistent sensory noise level. As indicated before, the results revealed a significant interaction between motion direction and the probability of rightward motion. Participants exhibited shorter RTs when their predictions were in accordance with the presented motion direction. Conversely, unexpected events were associated with longer responses. This finding aligns with the information-theoretic framework, which posits that unexpected events require greater cognitive effort, as evidenced by longer RTs (Zénon et al., 2019). This result was replicated in the second experiment. In this pilot study, we expanded our investigation by manipulating not only the probability of rightward motion but also the level of sensory noise (i.e., motion coherence). Consistent with well-established research on the impact of sensory uncertainty in motion perception, a clear pattern emerged, revealing that increased coherence levels correlated with faster responses (i.e., shorter RTs) and greater accuracy. Furthermore, following a visual inspection of the interaction plots, another noteworthy pattern becomes evident: the interaction between direction and probability of motion direction becomes more pronounced as the coherence level increases. This pattern is in contrast with our initial hypothesis, which posited that observers predominantly lean on predictions when stimuli have a high level of sensory noise.

Nevertheless, this observation can be elucidated through the foundational tenets of drift-diffusion models. Within sensory noisy situations, individuals are more likely to wait longer, delaying their decision-making to accumulate more evidence. A noisy stimulus—illustrated by the conditions of 15% and 25% motion coherence in this study— by virtue of containing minimal evidence compared to a noise-free signal (100% motion coherence), prolongs the information uptake (i.e., "drift rate" in drift-diffusion model terminology). Indeed, participants seemed to adopt a strategy of withholding their responses in situations of ambiguity, rather than exclusively relying on their predictions. In an uncertain and changing environment, individuals have a propensity to flexibly switch between strategies, for example transitioning from exploitation to exploration strategies (Aston-Jones & Cohen, 2005; Laureiro-Martínez et al., 2015). Consequently, individuals might opt to explore new behavioural avenues (exploration) while simultaneously capitalising on established knowledge (exploitation) and predictive inner models. It can be speculated that even if the participant holds expectations regarding the most probable direction, the presence of noisy stimuli causes the inherent sensory uncertainty to

overshadow the influence of the predictions on behaviour. In fact, the identification of unexpected uncertainty stands out as a significant cue, signalling the necessity to foster exploratory tendencies, and it assumes a pivotal role in the cultivation of adaptive behaviours within dynamically evolving environments (Bland & Schaefer, 2012). This does not negate the possible existence of a probability-induced effect on performance; rather, participants appear inclined toward information acquisition rather than unreservedly relying on predictions. This behaviour could also be viewed as adaptive because it may imply a recognition that the environment lacks stability (i.e., high volatility), meaning that, even if predictions hold temporarily, they could eventually lose accuracy. Conceivably, if the probabilities would have remained constant throughout the entire task (i.e., low volatility), the participant might find complete confidence in their inner predictive model, particularly in conditions of sensory uncertainty. A stable environment, as established by Behrens et al. (2007) does yield highly accurate predictions, leading to greater confidence in one's expectations (Meyniel, 2020). It is crucial to note that this study is preliminary in nature, and thus further tests and analyses are imperative to validate these observations.

Limitations and Future Directions

One limitation of the second study was the absence of manipulation concerning coherence levels other than those set at 15%, 25%, and 100%. The proximity between the 15% and 25% conditions limited the depth of insights that could be gained from their differences. Particularly intriguing is the potential to ascertain whether this trend of diminished predictive influence within conditions of high sensory uncertainty can be observed across other levels of motion coherence. Therefore, the inclusion of a coherence level situated between 100% and 25% will show potential for providing further insights into this phenomenon.

Furthermore, Experiment 2 does not include an adaptive procedure. As mentioned earlier, this technique plays a crucial role in "standardising" the task's difficulty across all participants, guaranteeing that each individual adequately perceives the global movements presented in the subsequent phase (experimental phase). This is essential to ensure participants' learning of the direction probabilities. Nonetheless, employing a linear mixed model enabled us to account for both the fixed effects (assumed to be uniform across all subjects) and, more importantly, the random effects (assumed to capture predictor effects specific to each subject).

Another drawback lies in the Bayesian model utilised. Since it is an ideal observer the right Bayesian probability does not consider the possibility that each participant might learn the

experimental volatility in a diverse manner. Furthermore, delving into the interplay between predictions about stimulus occurrence probability and sensory uncertainty calls for an approach surpassing behavioural analysis. Indeed, another limitation of this study resides in its behavioural nature, providing a partial glimpse into cognitive mechanisms, as it does not encompass their underlying processes at the neural level.

To gain a comprehensive understanding of the role that predictions play in decision-making, our next step will involve harnessing electroencephalogram (EEG) and eye-tracking methodologies. For instance, leveraging eye-tracking analysis can elucidate whether pre-existing expectations concerning motion direction contribute to the refinement of accuracy in smooth pursuit eye movements[15]. The predictive components of smooth pursuit eye movements have indeed been an area of exploration in previous research (e.g., Kim et al., 2019; Kowler et al., 2014). Moreover, pupillometry could shed light on the arousal state in the brain (de Gee et al., 2014; McGinley et al., 2015; van Kempen et al., 2019). Recent research has shown that central arousal variability has a significant impact on decision-making. The global arousal state is controlled by modulatory neurotransmitter systems such as the noradrenergic locus coeruleus (LC) and the cholinergic basal forebrain (de Gee et al., 2014, 2017; Larsen & Waters, 2018; Pfeffer et al., 2018; van Kempen et al., 2019). Recent inquiries have delved into the intriguing interplay between pupil dilation and nuanced facets of decision-making, such as *decision uncertainty*[16] (Urai et al., 2017), *decision bias*[17] (de Gee et al., 2014, 2017), *surprising events* (Preuschoff et al., 2011) and *volatility* (Bland & Schaefer, 2012). Furthermore, considering the distinct temporal scales at which these neuromodulatory systems function might elucidate the timing at which each piece of information is employed for deciding (de Gee et al., 2017). This, in turn, facilitates a heightened precision in the analysis of the relationship between predictions and sensory uncertainty. Pupil metrics can also predict the influence of new data on subsequent inferences. Tonic pupil response (i.e., baseline pupil diameter) was related to the reliability of the current data to be representative of the current state of the data (Nassar et al., 2010). Bland & Schaefer, (2012) suggested that the tonic activity of locus coeruleus (LC) may potentially mirror environmental volatility resulting from frequent shifts in behavioural strategies. Given

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[15] Smooth pursuit eye movements are a type of controlled, continuous, and fluid ocular motion that individuals use to track and follow moving objects.

[16] Decision uncertainty is defined by Urai et al. (2017) as "the probability a choice is correct, given the available evidence". As a consequence, it is closely intertwined with the level of confidence an individual has in a decision.

[17] De Gee et al. (2017) defined decision bias as "the degree to which an observer's choice deviates from the objective sensory evidence."

the described effect of volatility context on learning rate (Behrens et al., 2007), the purpose of the next step will be to correlate HGF parameters with participants' pupil response. Specifically, the RTs will be inserted as a response model in the HGF to estimate the learning rate parameters for each subject and to correlate these measures to their tonic pupil responses. This will enable us to harness the capabilities of HGF, which can avoid assuming a uniform fixed learning process across all subjects by extracting parameters tailored to each individual. Furthermore, the goal will also be to examine if the prediction trajectory of the ideal Bayesian observer correlates with the phasic pupil responses.

An additional avenue for future exploration involves the integration of EEG recordings. Concerning EEG activity associated with various aspects of decision-making, Kopp and colleagues (2016) provided an overview of ERP studies. From the experiments analyses emerged that amplitude fluctuations in the frontally distributed P3a are linked to Bayesian updating, indicating changes in prior probabilities due to the gradual accumulation of new evidence. In contrast, amplitude fluctuations in the parietally distributed P3b are associated with surprise, reflecting the unexpected nature of the evidence. Furthermore, Kelly & O'Connell (2013) employed a continuous version of the Random Dot Kinematogram (RDK), transitioning from incoherent to coherent motion. Their investigation revealed that the ERP component called centroparietal positivity (CPP) exhibited a gradual accumulation, leading to a standardised waveform pattern upon commitment to a selected alternative. This correlated with the strength of sensory evidence and predicted RTs.

Conclusions

In summary, our findings have illustrated that perceptual decision-making is not solely driven by bottom-up processes but predictions also play a pivotal role in performance as postulated by the Bayesian brain hypothesis. Given the limitations of our studies, future research will take a more comprehensive approach to examining these phenomena of interest. This will involve recording and analysing ERPs and spectral perturbations to meticulously study pre-stimulus oscillatory activity and functional connectivity. The objective is to elucidate how the internal states of the inner predictive model manifest in the states of the brain, thereby shaping subsequent model updating. Furthermore, given the influence of neuromodulators on brain states (de Gee et al., 2014, 2017; Larsen & Waters, 2018; Pfeffer et al., 2018; van Kempen et al., 2019), a comprehensive exploration will encompass investigating trial-to-trial fluctuations in eye movements and pupil dilation.

In conclusion, this thesis has illuminated the profound influence of predictions on behaviour within the context of a visual motion task. Our findings align with the Bayesian perspective, offering empirical evidence for the notion that perceptual decision-making is a product of the intricate interplay between bottom-up and top-down processes. Throughout our investigation, we have unveiled the remarkable capacity of the human cognitive system to autonomously and continuously monitor the underlying statistical patterns that govern our environment, even when explicit instructions are absent. Predictions and the assessment of volatility have emerged as pivotal components within the framework of perceptual decision-making, reshaping our understanding of this field in a manner that was previously overlooked. While the assertion regarding the impact of prediction on decision-making may appear self-evident, previous investigations have traditionally omitted the incorporation of top-down cognitive processes or the integration of learning regarding volatility. This conspicuous gap in the literature underscores the novelty and importance of our findings. Our research contributes to a deeper comprehension of perceptual decision-making processes and underscores the imperative need for future investigations to consider these critical factors. Consequently, the substantial impact of predictive mechanisms on behaviour opens new avenues for exploring the role of predictions in various aspects of decision-making and paves the way for future investigations into the neural underpinnings of these processes.

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