

# Neurally-informed modelling of static and dynamic decision biases

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## Abstract

Different accounts have been developed to explain the mechanisms underlying value biases during perceptual decision-making, within the model framework of bounded accumulation. The starting point bias account suggests a shift in the starting point of evidence accumulation, in the direction of the more valuable alternative. The drift rate bias account suggests that the mean rate of accumulation is steepened for the more valuable alternative. While most studies have supported a starting point bias (SPB) approach, recent work (Afacan-Seref, Steinemann, Blangero, & Kelly, 2018) suggests that drift rate biases (DRB) may also be applied in certain circumstances. Here, we used human EEG signatures of competitive motor preparation to construct a cognitive decision model that can explain the biasing mechanisms through which participants perform a value-biased orientation discrimination task under a strict deadline. Motor preparation dynamics showed signs of a value bias that emerged prior to evidence onset and increased steadily with time. Accordingly, we constructed a model that included an anticipatory dynamic urgency signal towards the High Value alternative. This model provided a better fit to behaviour than models with either a starting point or a drift rate bias but no anticipatory dynamics. These results point to a role for value-modulated, anticipatory motor preparation in fast-paced decision-making tasks, and suggest a unitary mechanism that can generate both static (starting point) and dynamic (drift rate) biases at the same time.

**Keywords:** value-biased decisions, urgency, decision making.

## Introduction

Simple perceptual decisions can be divided into three key processing stages: sensory encoding (the representation of sensory information in the brain), decision formation and motor execution. Under no time constraints, sensory encoding and decision formation can typically be completed well in advance of motor execution. However, in many real-life situations, such as when playing football or driving at speed in traffic, the brain has a limited time to integrate sensory information before a response must be produced. In such situations, motor processes must evolve swiftly and prioritise the action associated with higher value in order to maximise overall expected rewards, at the cost of greater uncertainty about the correct choice. The way in which the brain implements such prioritisation remains unclear.

For decades, sensorimotor decisions (where perception is translated into overt action) have been studied using Bounded Evidence Accumulation models. In this framework, sensory evidence is integrated over time into a “decision variable”, that produces an action upon reaching a threshold. Different model variants have been devised to explain why choices tend to be biased towards the more valuable option. The most prominent of them incorporate static biases that do not change in time, such as the Starting Point Bias (SPB) model, where the starting point of the decision variable is shifted towards the higher value option. The main alternative to this is a Drift Rate Bias (DRB), where the mean rate of accumulation is biased by value, and results in an increasing displacement of the decision variable with time. In principle, one way that a DRB can arise is from an enhancement of representations of higher-value alternatives at the sensory level or in the weighting of their readout, because stronger sensory evidence would lead to a steeper build-up of its integral. Another way is through the addition of a dynamic bias signal at the motor level, known as urgency. Urgency is an evidence-independent component of decision variable buildup that contributes to bringing the neural activity closer to a given neural threshold even in the absence of informative sensory evidence (Hanks, Kiani, & Shadlen, 2014). The decision-making literature reflects a preference for static (starting point) biases, because the models that incorporate them usually offer an excellent quantitative fit to response time (RT) distributions across many psychophysical tasks (Ratcliff & McKoon, 2008; Hawkins, Forstmann, Wagenmakers, Ratcliff, & Brown, 2015).

Although not favoured in cognitive model comparisons, other evidence suggests the plausibility of drift rate biases. For example, studies have shown that sensory cortical representations of stimuli are altered through their association with reward, in a manner resembling effects of spatial or feature-based attention (Serences & Saproo, 2010; Stanisor, Van Der Togt, Pennartz, & Roelfsema, 2013). There has also been em-

pirical evidence for the operation of dynamic urgency, which has been observed in the firing of neurons associated with motor preparation in saccade-decision tasks in monkeys (Hanks, Mazurek, Kiani, Hopp, & Shadlen, 2011). In that study, the authors used a motion discrimination task, where they manipulated stimulus reliability and the prior probability of motion direction. Their results showed that a model incorporating a dynamic bias signal that adds to cumulative evidence and increases as a function of decision time - effectively generating a DRB - provided a significantly better account of the data than a static signal implemented as a SPB.

In a recent human EEG study of rapid color discrimination under a very strict deadline, it was shown that a DRB model in which a constant value-bias is added to an increasing drift rate outperformed both standard SPB and DRB models (Afacan-Seref et al., 2018). This model could predict both behaviour and the temporal dynamics of neurophysiological signals reflecting decision formation. In particular, the model was able to capture a sudden, stimulus-evoked deflection in relative motor preparation initially towards the higher-value alternative, which, for low-value stimuli, was dynamically redirected toward the correct alternative. The model explained this by assuming that value biases are applied to sensory responses that are initially nonselective for color and become gradually more selective. In this way, the drift rate of the decision process, assumed to be driven by the difference in responses tuned to the two sensory alternatives, is initially dominated by value and later dominated by sensory information, as observed in the motor preparation dynamics.

Since the preceding model required assuming a two-phase sensory response that first detects (via nonselective activity) and then increasingly discriminates the sensory change being decided on, the question naturally arises, whether drift rate biases are peculiar to this situation, or are more generally invoked for any sensory feature when task demands require prioritisation. It has been shown that orientation-tuned neurons in the V1 region are immediately selective - that is, they respond quickly and vigorously to their preferred orientation and respond little if at all for the orthogonal orientation (Shapley, Hawken, & Xing, 2007). In this study, we therefore used an orientation discrimination task in order to assess the generality of drift rate biasing mechanisms when responding to sensory stimuli under time pressure.

Several lines of work have established that action selection dynamics at the motor level provide a key window onto the evolving decision process, because evidence accumulation is continuously fed to motor circuits (Selen, Shadlen, & Wolpert, 2012). For example, an fMRI study found a lateralized activation of the primary motor cortices since the very beginning of the evidence accumulation process (Gluth, Rieskamp, & Büchel, 2013). These authors also found that activity in the pre-supplementary motor area (pre-SMA) increased with time and was correlated with total accumulated evidence. This continuous involvement of the motor system during the decision-making process has been extended

to value-biased decisions, where it has been shown that the Lateralized Readiness Potential (LRP), an event-related potential thought to reflect the relative degree of preparation to move the left versus right hand (Kornhuber & Deecke, 1965; Vaughan, Costa, & Ritter, 1968) reflects the ongoing process of evaluating the incoming sensory information from its very beginning (Noorbaloochi, Sharon, & McClelland, 2015).

Studies such as Gratton et al. (1988), Van Vugt et al. (2014) and Noorbaloochi et al. (2015) found evidence for static SPB signals reflected in the LRP component, which were strongly associated with response outcomes. In particular, Noorbaloochi and colleagues showed that separate evidence related and reward related components could be clearly distinguished in the LRP signal. These features make this signal a great candidate for the analysis of our task.

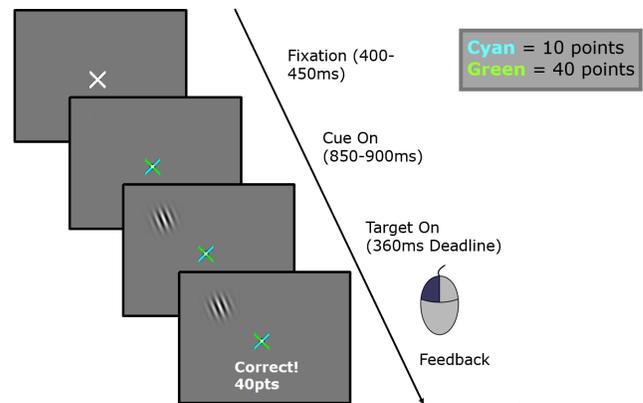


Figure 1: Orientation discrimination task.

In the present study we examined the static and/or dynamic biases at play in sensorimotor decisions under conditions of intense speed pressure. For this purpose, we recorded EEG activity during a value-biased orientation discrimination task under a strict deadline (Figure 1), where a correct response to one orientation was worth more (40 points) than to the other (10). We developed a bounded accumulation model informed by value-biasing signatures in the LRP and compared its fit to behaviour with that of existing models.

## Method

A total of 25 participants took part in the study, but 3 were excluded from the analyses due to inadequate EEG signal quality. They were compensated with €32 for their participation and they could earn up to €12 depending on their performance. They all had normal or corrected-to-normal vision and gave informed consent to participate in the study which was approved by our local ethics committee.

In the task, after the initial fixation, a cue (two crossed, coloured lines) was presented at fixation to indicate which of the two alternatives was worth more points (40 vs 10) if it was to be presented and responded to correctly, though the orientation actually presented was equally likely. The trial's value

was randomised and each block contained an equal amount of High and Low value trials. 850-900ms following the cue, an oriented grating target appeared on the upper left or upper right of the screen (fixed within a block and counter-balanced across blocks). The appropriate amount of points was awarded if a left or right-hand response was made to a left-tilted or right-tilted grating, respectively, within a 360-ms deadline. The main EEG recording consisted of 8 blocks of 160 trials each.

Motor preparation was measured as the LRP (Gratton et al., 1988; de Jong, Wierda, Mulder, & Mulder, 1988; Eimer, 1998), at standard EEG sites C3 and C4. Four simplified versions of the bounded diffusion models were constructed to examine the two alternative value biasing mechanisms (SPB and DRB) and also to examine the mechanisms that produce fast errors (starting-point variability ['VS'] versus increasing evidence ['IE']) as was done in Afacan-Seref et al. (2018). The SPB-VS model was defined by the following equation:

$$\begin{aligned} x(t) &= x(t-1) + d \cdot dt + N(0, s\sqrt{dt}) \\ x(0) &\sim \mathcal{U}(\pm z_B, \pm z_B + s_z) \end{aligned} \quad (1)$$

Where  $d$  is the drift rate,  $dt$  is the discrete time increment (1 ms in simulations) and  $N(0, s\sqrt{dt})$  refers to Gaussian noise with zero mean and variance  $s^2 \cdot dt$ . The SPB is  $z_B$ , with a positive sign for High Value and negative for Low Value trials. The starting point variability was determined by  $s_z$ . The DRB-VS model was defined by the following equation:

$$\begin{aligned} x(t) &= x(t-1) + (d \pm d_B)dt + N(0, s\sqrt{dt}) \\ x(0) &\sim \mathcal{U}(-s_z, +s_z) \end{aligned} \quad (2)$$

Where  $d_B$  is the symmetric bias in the drift rate (positive for High Value trials and negative for Low Value ones). The SPB-IE model was defined by:

$$\begin{aligned} x(t) &= x(t-1) + c \cdot t \cdot dt + N(0, s\sqrt{dt}) \\ x(0) &= \pm z_B \end{aligned} \quad (3)$$

Where  $c$  is the slope for the linearly increasing drift rate. The DRB-IE model was defined by:

$$\begin{aligned} x(t) &= x(t-1) + (c \cdot t \pm d_B)dt + N(0, s\sqrt{dt}) \\ x(0) &= 0 \end{aligned} \quad (4)$$

A fifth model was created inspired by the observed LRP dynamics (see Results), which included an early biased dynamic urgency signal. This model was defined by:

$$\begin{aligned} x(t) &= x(t-1) + u \cdot dt + e(t)(d \cdot dt + N(0, s\sqrt{dt})) \\ x(u_{oT}) &= 0 \\ e(t) &= \begin{cases} 0, & \text{if } t < e_{oT} \\ 1, & \text{if } t \geq e_{oT} \end{cases} \\ u &\sim N(\pm u_\mu, u_\sigma) \end{aligned} \quad (5)$$

Where  $u$  is the rate of increase of the urgency signal. The onset time of the urgency signal is defined by  $u_{oT}$ . The mean of this urgency signal has a positive sign for High Value conditions and a negative one for Low Value ones. The appearance of the evidence and start of the accumulation process is represented by the unit step function  $e(t)$  with onset at  $e_{oT}$ . For all models the decision variable  $x$  evolved with the stated dynamics until it crossed either an upper (+1) or lower (-1) bound resulting in a correct or incorrect outcome, respectively, with the RT equated to the bound crossing time, such that any non-decision time is allowed for by the onset timing parameters  $u_{oT}$  and  $e_{oT}$ .

All models were fitted by Monte-Carlo simulation methods to individual participant choice and RT distributions with a bounded SIMPLEX routine (Nelder & Mead, 1965) implemented in the MATLAB function `fminsearchbnd` with a  $G^2$  likelihood ratio statistic as the cost function, quantifying the divergence between the bins separated by the five quantiles [1, 3, 5, 7, 9] for correct and error trials in the simulated and real datasets.

## Results

As expected, correct responses were more frequent on High Value than Low Value trials (90% versus 54%,  $F(1, 21) = 51.51, p < .001$ ; Figure 2). There was a significant interaction of value (high/low) x accuracy (correct/error) on RT ( $2 \times 2$  rmANOVA,  $F(1, 21) = 600.45, p < .001$ ), driven by the fact that correct trial RTs were significantly faster for High Value targets compared to Low Value targets ( $t(21) = -76.773, p < .001$ ) and the opposite was observed for Errors ( $t(21) = 11.027, p < .001$ ). When plotting Accuracy over RT, a shift in the responses was observed for low value trials, from very fast, purely value-driven erroneous responses to slow sensory-driven correct ones (Figure 2). The fast value-driven responses are further emphasized by the perfect overlap in the leading tail of the distribution for Low value errors and High Value correct trials.

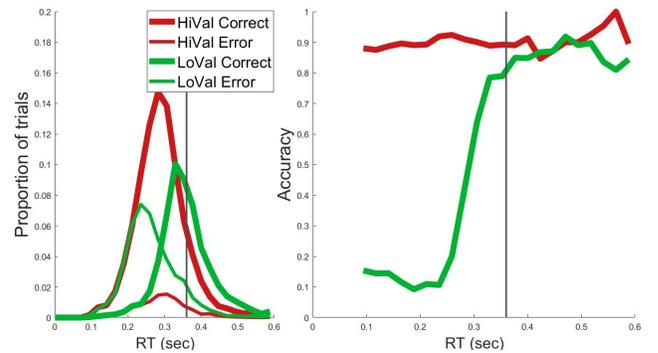


Figure 2: Response Time distribution and Conditional Accuracy Function averaged over participants.

A bias mechanism in the form of a SPB around target onset was observed in the LRP (Figure 3), across the dif-

ferent value conditions ( $F(1, 21) = 21.583, p < .001$ ) and it had an influence on choice outcome (for Low Value trials  $F(1, 21) = 6.88, p = 0.016$ ). Interestingly, this bias in starting level at target onset did not appear to be static, but continuously grew through the post-target delay period before the process accelerated due to bottom-up input. This reflects a dynamic urgency bias (value difference in the slopes of the target locked LRP from -100 to 100ms  $t(21) = 4.6, p < .001$ ; Figure 3) and represents an empirical neural signature of DRB. We used this anticipatory urgency signal from the LRP to estimate an “urgency onset time” that we could compare to the urgency onset time estimated by our model (Table 1). A straight line was fitted to the target-locked LRP signal from -100ms to 100ms and extended backward in time until it reached zero, producing an estimate of the starting point of this dynamic bias: around 442ms before target onset. This empirical urgency onset time differed from the model’s estimation (-442ms vs 72ms). Response-locked LRP plots showed a pre-response “threshold” level that did not significantly vary with value ( $F(1, 21) = .547, p = .468$ ) or location ( $F(1, 21) = .250, p = .622$ ). This was consistent with our model’s assumption of constant bounds set above and below a one-dimensional decision variable.

Table 1: Estimated parameter values for the Urgency model, averaged across participants.

$u_{oT}$	$u_{\mu}$	$u_{\sigma}$	$d$	$s$	$e_{oT}$
0.072	3.0342	4.205	9.973	2.839	0.27

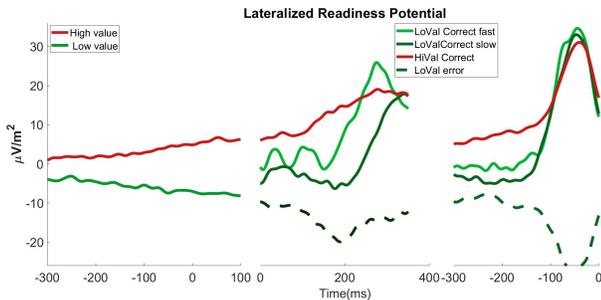


Figure 3: From left to right, LRP motor preparation dynamics time-locked to the target onset for High and Low value (left), separating Fast and Slow Low Value (center), and time-locked to the response (right), broken out by behavioural outcome. Upward deflections reflect preparation toward the correct response.

As in previous work (Afacan-Seref et al., 2018), a DRB model with increasing evidence showed a better fit to behaviour (lower Bayes Information Criterion [BIC], Figure 4) than SPB models, or models that included variability in their starting point rather than increasing evidence. However, our neurally-informed model, which instead incorporated an an-

tipatory biased urgency signal and time-invariant but later-onsetting evidence, provided the best fit overall (lowest BIC, Figure 4).

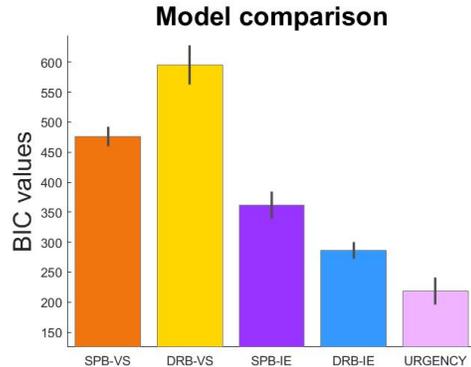


Figure 4: Mean BIC values quantifying goodness of fit. Error bars indicate S.E.M. after factoring out between-subjects variance.

## Discussion

When faced with different environmental demands, choice-associated rewards need to be taken into account to make a decision that maximises expected gain. Within the stream of processes that lead to an action, at what point is this reward exerting its influence? What neural mechanism is responsible for it? Answering these questions and providing a neurally informed model that can capture behaviour in time-constrained situations is key to guiding leading theories about cognitive dysfunction in brain disorders such as ADHD, Autism, Depression, Addiction, Borderline Personality Disorder, Obsessive-Compulsive Disorder, and Parkinson’s disease.

In this study, we examined behaviour and motor preparation dynamics during a two-choice rapid orientation discrimination task with asymmetric rewards (10 vs 40 points). Neurally informed mathematical modelling indicated that both static and dynamic biases are needed to explain behavioural data in fast decision scenarios and that the effects of both can be generated through a unitary mechanism, namely an anticipatory biased urgency signal.

Despite the prevalence of studies supporting static biases over dynamic ones for many years, recent studies are suggesting that dynamic biases might also play a role in the decision making process, especially when faced with time restrictions (Afacan-Seref et al., 2018). However, the literature already held examples of mixed results. On the one hand, for example, Ratcliff and McKoon (2008), used a biased motion discrimination task in which stimulus proportion for left or right responses was varied. The authors interpreted a shift in the leading edges of the RT distributions due to stimulus probability, as an indication of a SPB. This conclusion was also supported by their model, which showed that the differ-

ence in starting point accounted for most of the proportion effect. On the other hand, in one monkey single-cell recording study (Hanks et al., 2011) using a motion discrimination task, firing rates of decision variable encoding sensorimotor neurons built at a steeper rate toward the more probable option. They thus constructed a model that included a dynamically growing, evidence-independent bias component, which was able to account for human and monkey behaviour better than standard models. Although this bias signal would effectively implement a DRB, this interpretation was not universally accepted (Ratcliff, Smith, Brown, & McKoon, 2016). The model we constructed here is very similar but has the distinction that, as reflected in motor preparation dynamics, the biased urgency signal can, under time pressure, be well under way before the evidence begins to be processed. In doing so, we demonstrate that both starting point biases and drift rate biases are at play in the same scenario and can be generated by a single mechanism.

Accurately adjudicating between alternative cognitive models of the decision process can be difficult based on behaviour alone (O'Connell, Shadlen, Wong-Lin, & Kelly, 2018). In the present study, we used neural data to inform the structure and the fitting process of our models. A dynamic bias signal observed in the LRP, which started before evidence onset, effectively producing a SPB as well, indicated that an anticipatory urgency signal must have been at play. This is well expected in such a fast-paced task where the participant has very limited exposure to the stimulus before the deadline. Also, a unique threshold was observed in the motor preparation dynamics across conditions, inspiring the construction of a one-dimensional decision model.

It has been suggested that top-down expectations could influence the creation of representations or templates of the expected stimulus in the visual cortex, and these representations would later be compared to bottom-up stimulus information (Friston, 2005; Rao & Ballard, 1999; Mumford, 1992). Neural responses to redundant (expected) information in early sensory regions might be suppressed by higher-order regions (Mumford, 1992; Murray, Kersten, Olshausen, Schrater, & Woods, 2002; Rao & Ballard, 1999) or they could be rather increased by suppressing responses to stimuli that are inconsistent with the current expectations (Lee, Yang, Romero, & Mumford, 2002). Value biases could influence the creation of such representations as expectations do (Stanisor et al., 2013), by means of changing the drift rate during the decision making process. Alternatively, a modulation of the weighting or reference values used in the readout of these sensory representations could cause a change in the drift rate (Afacan-Seref et al., 2018). The present results can neither prove nor exclude the possibility that biases are also exerted at the sensory level or its readout. Further studies looking into an explicit modulation of the early visual cortical responses are needed in order to answer this question.

However, we found evidence for the third possibility mentioned above, a simpler mechanism that can produce drift rate

biases that originate at the motor level (urgency). Up to now, motor preparation dynamics have been shown to reflect the continuous evaluation of incoming sensory information only from the beginning of the evidence accumulation process, assumed in standard models to onset after sensory encoding has been completed (Ratcliff & McKoon, 2008). However, our results suggest that decision-related motor preparation dynamics are in play well before the evidence is encoded, and that under time constraints, reward information is fed to the motor circuit to bias these anticipatory dynamics independent of the evidence presentation. This finding bears some similarity to Noorbaloochi et al. (2015) where separate evidence and reward related components were observed in the LRP, but our model is distinct in that rather than assuming two separate value-biased guess and sensory accumulation processes, reward information and sensory evidence jointly influence a single, dynamically evolving decision process. That there is a single, thresholded process is evidenced in the unique decision threshold that we observed in the LRP across value conditions (Figure 3).

In our study, unlike Noorbaloochi et al. (2015), the anticipatory urgency bias did correlate with response choice (see Results). This discrepancy could be caused by the different deadlines used in each study. Here, the deadline was very tight and to perform optimally you needed to start preparing before seeing the stimulus on the screen. In fact, our neural data suggest that this preparation started  $\sim 442$ ms before stimulus onset and continuously grew over time, whereas in Noorbaloochi et al. (2015), the SPB was static, and their model estimated that the fast guess process onsets at  $\sim 150$ ms after target onset. In fact, our own model's estimated parameter for the start of the urgency signal (0.072 s) did not coincide with our neural data. Even accounting for the fact that our onset estimate would be misestimated to be later by an amount equal to the motor non-decision time, the latter can be expected to be approximately 50-100 ms, leaving still a big discrepancy between the empirical and the estimated data. A possible next step could be to constrain the model, in order to match this urgency onset time and test whether it is still able to account for the behavioural dynamics. So far, the present model presents one unique mechanism that can qualitatively account for the increase in Starting Point Bias observed in the LRP and quantitatively capture the observed RT distributions.

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