

# 1 Multiphasic value biases in fast-paced decisions

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9 **Abstract** Perceptual decisions are biased toward higher-value options when overall gains can be  
10 improved. When stimuli demand immediate reactions, the neurophysiological decision process  
11 dynamically evolves through distinct phases of growing anticipation, detection and discrimination,  
12 but how value biases are exerted through these phases remains unknown. Here, by parsing motor  
13 preparation dynamics in human electrophysiology, we uncovered a multiphasic pattern of  
14 countervailing biases operating in speeded decisions. Anticipatory preparation of higher-value  
15 actions began earlier, conferring a “starting point”- advantage at stimulus onset, but the delayed  
16 preparation of lower-value actions was steeper, conferring a value-opposed buildup rate bias. This,  
17 in turn, was countered by a transient deflection toward the higher value action evoked by stimulus  
18 detection. A neurally-constrained process model featuring anticipatory urgency, biased detection,  
19 and accumulation of growing stimulus-discriminating evidence, successfully captured both behavior  
20 and motor preparation dynamics. Thus, an intricate interplay of distinct biasing mechanisms serves  
21 to prioritise time-constrained perceptual decisions.

## 22 Introduction

23 Perceptual decision making is generally well explained by a process whereby evidence is  
24 accumulated over time up to a bound that can trigger an action (Brown and Heathcote, 2008; Link  
25 and Heath, 1975; Ratcliff, 1978; Smith and Ratcliff, 2004; Usher and McClelland, 2001). In most  
26 models based on this principle, a given response time (RT) is made up of two temporal  
27 components, where the decision variable is either building at a stationary rate (“drift rate”)  
28 determined by a stable evidence representation, or is suspended, during “non-decision” delays  
29 associated with sensory encoding and motor execution. This simple scheme, developed primarily  
30 through the study of slow, deliberative perceptual decisions, affords two ways to explain how faster  
31 and more accurate responses are made to higher-value or more probable stimuli: through  
32 modulating the starting point or drift rate of the process (Feng et al., 2009; Leite and Ratcliff, 2011;  
33 Mulder et al., 2012; Ratcliff and McKoon, 2008; Simen et al., 2009; Summerfield and Koechlin,  
34 2010; Urai et al., 2019; Voss et al., 2004; White and Poldrack, 2014). Corresponding adjustments  
35 have been reported in neurophysiological recordings from motor-related areas of the brain (de  
36 Lange et al., 2013; Hanks et al., 2011; Rorie et al., 2010). However, recent work has highlighted  
37 additional dynamic elements of the decision process whose contributions to choice performance are  
38 likely to be accentuated when stimuli require immediate action.

39 First, when stimulus onset is predictable, anticipatory activity in motor preparation regions can begin  
40 to forge a decision even before the stimulus appears. While standard models do allow for  
41 anticipatory processing in the setting of the starting point from which the accumulator evolves after  
42 sensory encoding, neurophysiological data have revealed that anticipatory motor preparation is  
43 dynamic, proceeding on a trajectory aimed at eventually crossing an action-triggering threshold by  
44 itself even in the absence of sensory input (Feuerriegel et al., 2019; Kelly et al., 2020; Stanford et  
45 al., 2010). Such evidence-independent buildup components, often labelled as ‘urgency signals,’  
46 effectively implement a collapsing bound on cumulative evidence, so that decisions that continue

47 longer can be completed based on less evidence (Churchland et al., 2008; Hanks et al., 2014;  
48 Murphy et al., 2016; Shinn et al., 2020; Steinemann et al., 2018; Thura and Cisek, 2014).

49 Second, for many suddenly-onsetting stimuli, sensory evidence of their distinguishing features  
50 emerges some time after the initial sensory neural response signalling their onset (Afacan-Seref et  
51 al., 2018; Smith and Ratcliff, 2009), meaning that detection precedes discrimination. In the case of  
52 the widely-studied random dot motion stimulus, recent work shows that behavior is well captured by  
53 a model in which accumulation begins at the onset of sensory encoding but where it takes a further  
54 400 ms for the direction information to stabilise (Smith and Lilburn, 2020). In fact, serial detection  
55 and discrimination phases are reflected in human electrophysiological signatures of differential  
56 motor preparation during fast, value-biased decisions about other sensory features. Specifically,  
57 these signals show biased stimulus-evoked changes initially in the direction of higher value before  
58 being re-routed towards the correct sensory alternative (Afacan-Seref et al., 2018; Noorbaloochi et  
59 al., 2015), in line with previously proposed dual-phase models (Diederich and Busemeyer, 2006).

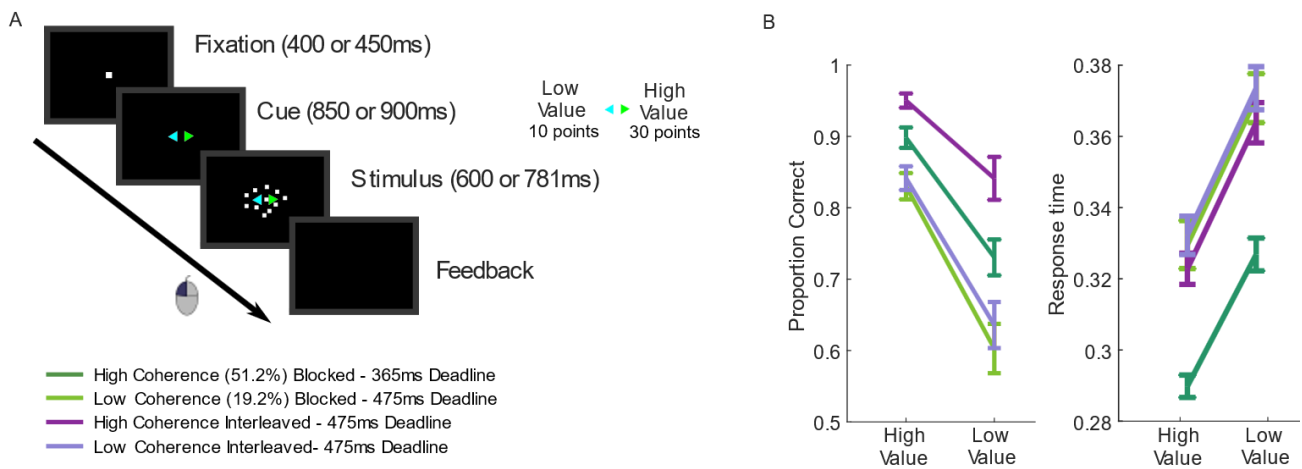
60 Thus, in time-pressured situations decision formation is not suspended until sensory  
61 representations stabilise, but rather proceeds through a concerted sequence of anticipatory,  
62 detection and discriminatory processing phases. Although previous work has established the  
63 potential importance of these individual phases (Afacan-Seref et al., 2018; Diederich and  
64 Busemeyer, 2006; Kelly et al., 2020; Noorbaloochi et al., 2015; Smith and Lilburn, 2020; Stanford et  
65 al., 2010), there exists no detailed computational account of how value-biased decision formation  
66 dynamics unfold through all three of them. In this study we used two complementary human  
67 electrophysiological signatures of motor preparation during performance of a sudden-onset random  
68 dot motion discrimination task under a tight deadline, to forge such an account.

69 We observed a complex pattern of distinct biases exerted across multiple phases including an initial  
70 anticipatory buildup in motor preparation for the high-value alternative, a later but steeper  
71 anticipatory buildup for the low-value alternative and then, immediately following stimulus onset, a  
72 further transient burst toward the high-value alternative. By incorporating urgency signal model  
73 components whose initial amplitude and buildup rate were constrained to match the corresponding  
74 measures of anticipatory motor preparation we were able to adjudicate among several alternative  
75 multi-phase decision process models. We found that a model that featured 1) an initial, transient  
76 detection-triggered deflection toward the higher value alternative and 2) gradually-increasing  
77 discriminatory sensory evidence, best accounted for behavior, as well as recapitulating the fast  
78 dynamics of stimulus-evoked, differential motor preparation. Together, the findings show that, rather  
79 than simply enhancing all parameters of the decision process in favour of high-value alternatives,  
80 the neural decision architecture has the flexibility to apply biases in opposing directions to different  
81 process components, in a way that affords low-value decision signals the chance to “catch-up”  
82 when smaller rewards can be attained.

## 83 Results

84 **Behavior.** Participants performed fast-paced motion direction discrimination using the well-studied  
85 random dot kinematogram (RDK) stimulus (Roitman and Shadlen, 2002) with a preceding cue  
86 indicating the more valuable direction. We recorded scalp electroencephalography (EEG) from  
87 seventeen participants performing the task in three blocked regimes: high coherence with a very  
88 short deadline; low coherence with a slightly longer deadline; and the two coherences interleaved  
89 with the longer deadline (Figure 1A). While we were primarily focused on the value biasing  
90 dynamics in common across these challenging regimes, these manipulations allowed us to further  
91 explore potential regime differences in the degree of the uncovered effects. In each trial, colored  
92 arrows appeared prior to the stimulus onset indicating the respective value of a correct response in  
93 the two possible directions (left and right), and participants responded by clicking a mouse button  
94 with their corresponding thumb. Correct responses between 100 ms after stimulus onset and the  
95 deadline resulted in the points associated with the color cue; otherwise, no points were earned.

96 The value manipulation produced strong behavioral effects. Accuracy was higher for high-value  
97 trials than low-value trials ( $F(1,16)=60.6$ ,  $p<0.001$ , partial  $\eta^2=0.79$ ), and the median RTs for correct  
98 responses were shorter ( $F(1,16)=80.9$ ,  $p<0.001$ , partial  $\eta^2=0.84$ ). These effects were manifest to a  
99 strong degree across all 4 conditions, though overall accuracy and RT varied (Figure 1B).



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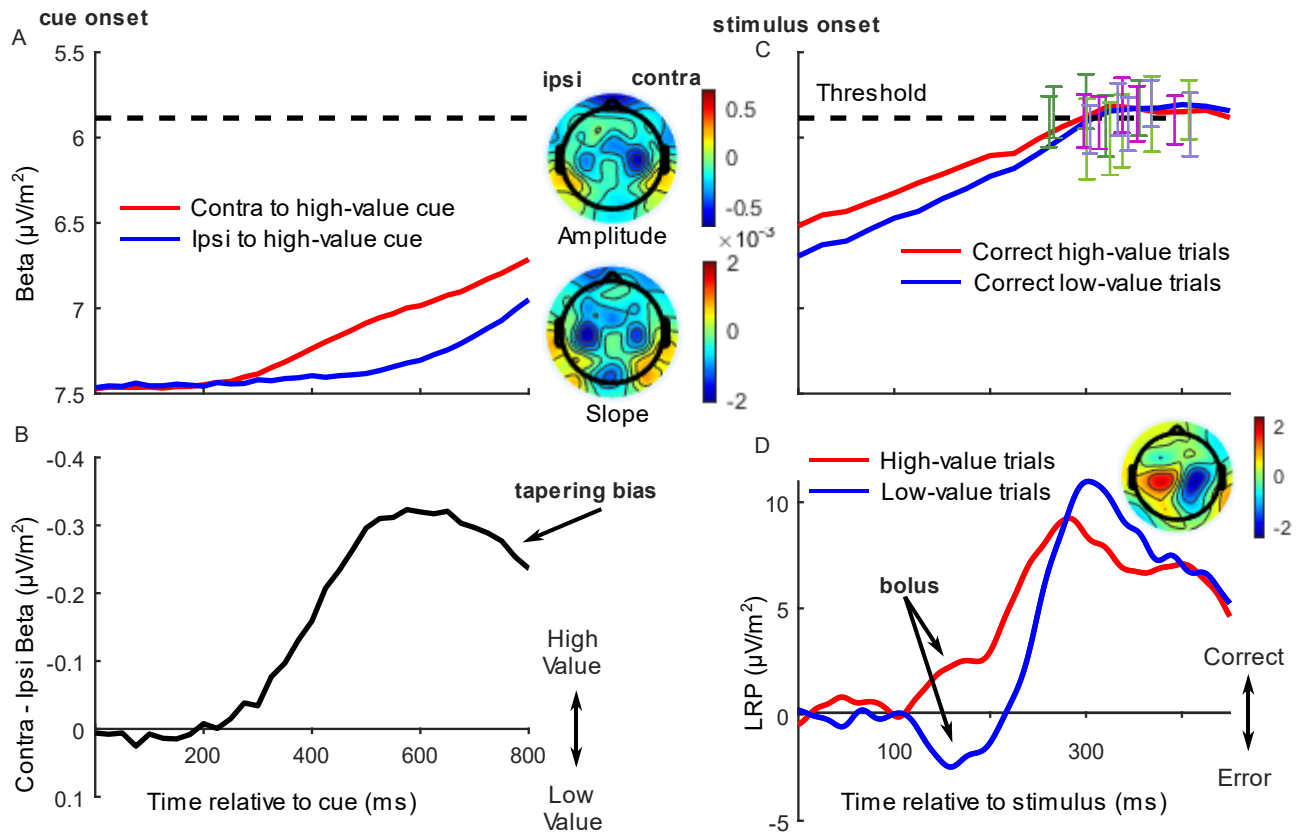
101 Figure 1: Value-cued motion direction discrimination task and behavioral data. A Trial structure with  
102 task conditions below. B Mean and standard error across participants for proportion correct and  
103 median RTs of correct responses. In addition to the large value effects, task condition affected  
104 accuracy ( $F(3,48)=60.3$ ,  $p<0.001$ , partial  $\eta^2=0.79$ ) and correct RTs ( $F(3,48)=38.1$ ,  $p<0.001$ , partial  
105  $\eta^2=0.71$ ); the high coherence conditions were more accurate ( $p<.001$  for blocked and interleaved)  
106 and the blocked high-coherence condition, with the shorter deadline, was the fastest ( $p<.001$   
107 compared to other 3 conditions). Pairwise comparisons revealed no significant difference between  
108 the two low-coherence conditions ( $p=0.1$ ,  $0.6$ ;  $BF_{10}=0.87$ ,  $0.28$  for accuracy and correct RTs  
109 respectively). The Condition  $\times$  Value interaction was significant for accuracy ( $F(3,48)=6.4$ ,  $p=0.005$ ,  
110 partial  $\eta^2=0.29$ ) but not correct RTs ( $p=0.7$ ).

111 **EEG Signatures of Motor Preparation.** To trace motor preparation for the left and right hand  
112 responses, from the period of stimulus anticipation through to response completion, we measured  
113 decreases in spectral EEG amplitude in the Beta band (integrated over 14-30Hz) at selected motor  
114 electrodes in the right and left hemispheres (Donner et al., 2009; O'Connell et al., 2012). Prior to  
115 stimulus onset, motor preparation began to build in response to the value cue, first for the high-  
116 value alternative and later for the low-value alternative ( $F(1,16)=18.9$ ,  $p<.001$ , partial  $\eta^2=0.54$  for  
117 jackknifed onsets, Figure 2A). Immediately before stimulus onset (750 ms after the cue) preparation  
118 for the high-value alternative was greater than that for the low-value alternative ( $F(1,16)=17.7$ ,  
119  $p<.001$ , partial  $\eta^2=0.53$ ). Despite their later onset, the buildup rates of motor preparation signals for  
120 the low-value alternative were significantly steeper, (slope from 700-800 ms,  $F(1,16)=9$ ,  $p=.008$ ,  
121 partial  $\eta^2=.36$ ). As a consequence of these differences in onset and buildup rate, the bias in relative  
122 motor preparation favouring the high-value cue peaked at around 600 ms post-cue and then began  
123 to decline before stimulus onset (Figure 2B). In keeping with previous observations (Kelly et al.,  
124 2020; O'Connell et al., 2012; Steinemann et al., 2018), motor preparation continued to build after  
125 stimulus onset, reaching a highly similar level at response irrespective of cue-type, coherence or  
126 regime contralateral to the chosen hand, consistent with a fixed, action-triggering threshold (Figure  
127 2C). The left- and right-hemisphere Beta signals thus reflected two race-to-threshold motor-  
128 preparation signals, whose anticipatory buildup was indicative of dynamic urgency that, independent  
129 of the evidence, drove the signals towards the threshold (Churchland et al., 2008; Hanks et al.,  
130 2014; Murphy et al., 2016; Steinemann et al., 2018; Thura and Cisek, 2014).

131 Next, to trace the rapid stimulus-evoked dynamics of the decision process with higher temporal  
132 resolution we examined the broadband lateralized readiness potential (LRP). This differential signal  
133 represents the relative motor preparation dynamics between the hands associated with the correct

134 and error responses (Afacan-Seref et al., 2018; Gluth et al., 2013; Gratton et al., 1988;  
135 Noorbaloochi et al., 2015; Van Vugt et al., 2014), here examined relative to a peri-stimulus baseline  
136 interval (-50-50 ms) in order to emphasise fast stimulus-evoked dynamics (Figure 2D; see also  
137 Figure 2-Figure Supplement 1 for an analysis of the pre-stimulus LRP). Beginning approximately  
138 100 ms after the stimulus, there was a deflection in the direction of the cued choice (in the correct  
139 direction for high-value trials and incorrect direction for low-value trials,  $F(1,16)=20.2$ ,  $p<.001$ , partial  
140  $\eta^2=.56$ , effect of value on the mean LRP from 150-180 ms, Figure 2D). We refer to this initial  
141 deflection as a “bolus,” following a similar finding by Noorbaloochi et al., (2015). The sensory  
142 evidence appears to begin to affect motor preparation at around 150 ms when the LRP for the low-  
143 value trials begins to turn around and build in the correct direction.

144 Together these signals indicate that motor preparation passed through several key phases.  
145 Anticipatory buildup began first for the high-value alternative, followed by low-value preparation  
146 which, beginning to compensate for its lower level, reached a higher buildup rate before stimulus  
147 onset, constituting a negative drift-rate bias. Then, stimulus onset evoked a brief value-biased  
148 deflection, consistent with a positive drift-rate bias effect, before giving way to a final phase  
149 dominated by discriminatory sensory information.



150

151 Figure 2: EEG signatures of motor preparation. A Unilateral Beta amplitude, contralateral to high-  
152 and low-value alternatives in the period after the cue and before the motion stimulus appeared at  
153 850 or 900 ms; Note that the Y-axis is flipped such that decreasing amplitude (increasing motor  
154 preparation) is upwards. Topographies are for left-cued trials averaged with the right-left flipped  
155 topography for right-cued trials, so that the right side of the head-plot represents the hemisphere  
156 contralateral to the high-value side. Amplitude topography reflects Beta amplitude at 750 ms relative  
157 to amplitude at cue onset, and slope is measured from 700-800 ms. B Relative motor preparation  
158 (the difference between the waveforms in panel A), highlighting the pre-stimulus decline due to  
159 steeper low-value urgency. C Beta amplitude contralateral to response for correct trials only, relative  
160 to stimulus onset. Error bars are the standard errors of amplitudes 50 ms before response, with  
161 between-subject variability factored out, plotted against RT. Trials were separated by session and



162 coherence, showing high- and low-value correct trials median-split by RT and low-value error trials.  
163 D LRP: ipsilateral - contralateral to correct response calculated at standard sites C3/C4, so that  
164 deflection upward corresponds to relative motor preparation in the correct direction. LRP waveforms  
165 were baseline corrected with respect to the interval -50-50 ms to focus on local stimulus-evoked  
166 dynamics. Topography shows the difference in amplitude between left- and right-cued trials at 150-  
167 180 ms relative to baseline. All waveforms derived from all trials regardless of accuracy unless  
168 otherwise stated.

169 **Model Development.** We next sought to construct a decision process model that can capture both  
170 behavior and the motor preparation dynamics described above. Mimicking the unilateral Beta  
171 signals, we modeled the decision process as a race between two parallel, accumulation-to-bound  
172 decision variable (DV) signals (Figure 3A), with distinct pre-stimulus starting levels set for the DV  
173 contralateral (parameter  $Z_c$ ) and ipsilateral ( $Z_i$ ) to the direction of the value cue for each regime.  
174 Extrapolating from the anticipatory motor preparation buildup, we assumed the operation of linearly-  
175 increasing urgency which was also biased by the value cue. The urgency buildup rates varied from  
176 trial to trial independently for the two response alternatives, in a Gaussian distribution with means  
177  $U_{c,i}$  and standard deviation  $s_u$ . We assume in all models that the accumulation process takes an  
178 additive combination of noisy stimulus evidence plus a stimulus-evoked bias, both of which are  
179 implemented in alternative ways for comparison as detailed below. We refer to that combination as  
180 the "cumulative bias plus evidence" function,  $x(t)$ . The DVs were then generated by adding the  
181 cumulative bias plus evidence in favor of either alternative to the corresponding urgency signal,  
182 triggering a decision at the "decision time" when the first reached the bound:

$$183 \quad DV_1(t) = DV_1(t - dt) + u_1 \cdot dt + [x(t)]$$

$$184 \quad DV_2(t) = DV_2(t - dt) + u_2 \cdot dt + [-x(t)]$$

185 Here  $DV_1$  and  $DV_2$  represent the DVs for the correct and incorrect responses respectively, which  
186 were updated in our simulations at a time interval  $dt = 1$  ms.  $u_1$  and  $u_2$  represent the urgency rates  
187 contralateral and ipsilateral to the cued direction on high-value trials, and the reverse on low-value  
188 trials. For example, in a high-value trial (in which the cued direction is the correct response):

$$189 \quad u_1 \sim N(U_c, s_u), \text{ and}$$

$$190 \quad u_2 \sim N(U_i, s_u).$$

191 The cumulative bias plus evidence,  $x(t)$  is positive in the direction of the correct response, and the  
192 half-wave rectification operation,  $[x] = \max(0, x)$ , apportions the positive and negative components  
193 to the appropriate DVs. In contrast to this approach, several authors have modeled urgency as a  
194 multiplicative "gain" function accelerating the decision process (Cisek et al., 2009; Ditterich, 2006;  
195 Evans et al., 2017; Standage et al., 2011; Thura et al., 2012). However, we considered additive  
196 motor-level urgency signals (Churchland et al., 2008; Hanks et al., 2014) that linearly increased with  
197 time (Murphy et al., 2016; Steinemann et al., 2018) to be the most natural interpretation of the Beta  
198 signals here due to their anticipatory buildup before evidence accumulation was possible.

199 The trial RT was obtained by adding to the decision time a *motor time* for motor execution; this  
200 varied from trial to trial on a uniform distribution with mean  $T_m$  which varied between the blocked  
201 regimes, and range  $s_t$ . Allowing for regime differences in motor execution was important as its  
202 timing is known to be affected by speed/accuracy settings (Kelly et al., 2020; Rinkenauer et al.,  
203 2004; Weindel et al., in press). In previous work we had constrained the mean motor time parameter  
204 using an EEG motor-evoked potential (Kelly et al., 2020). However, likely due to the substantially  
205 increased model constraints in the current study (see Neural Constraints section below), we found  
206 in preliminary analyses that constraining the motor times in this way was detrimental to our fits. The  
207 cumulative bias plus evidence function was updated according to the following equation:

208

$$x(t) = x(t - dt) + B(t).dt + \mu(t).dt + w(t).\sqrt{dt}$$

209

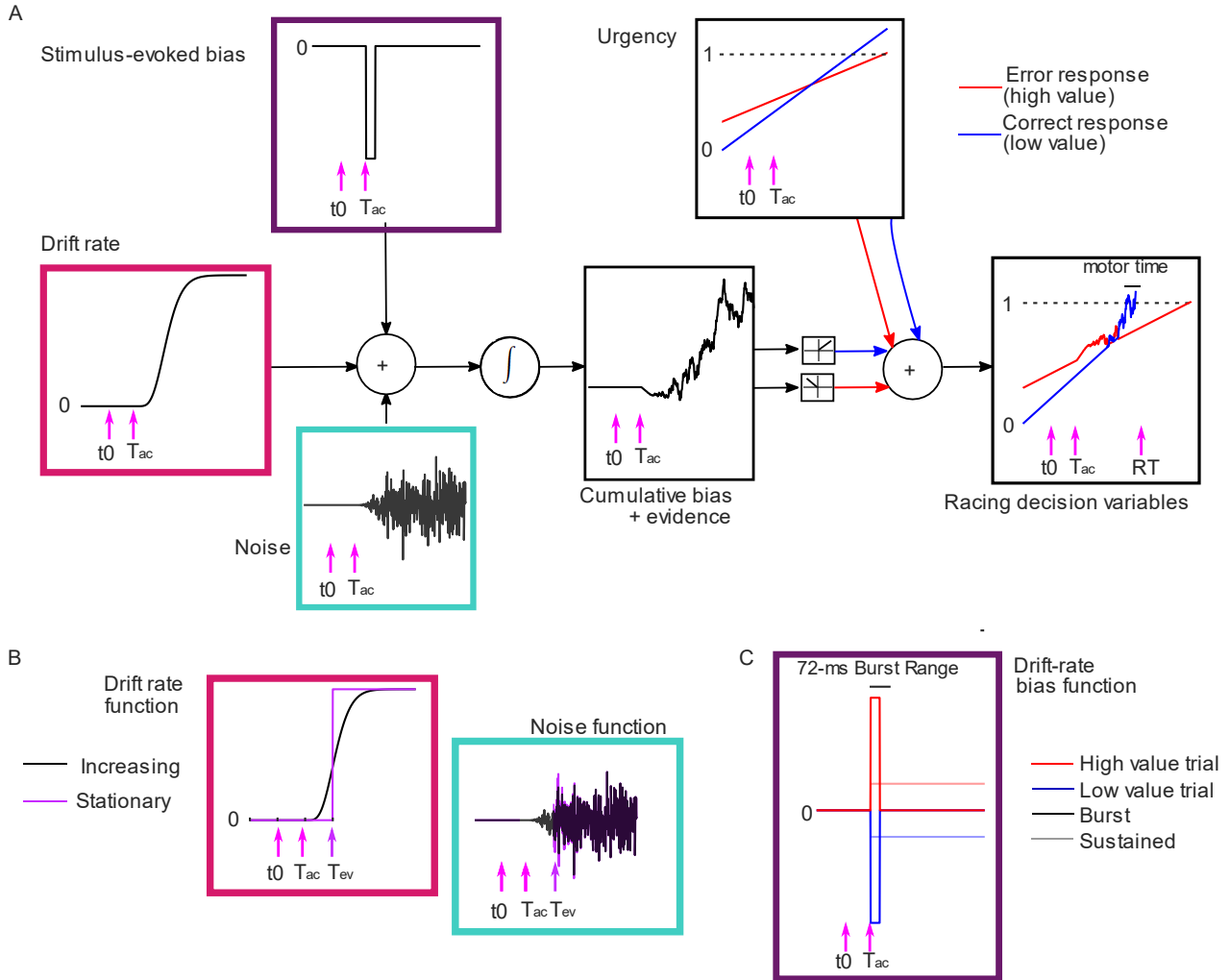
Here  $B(t)$  represents the stimulus evoked bias,  $\mu(t)$  is the drift rate of the evidence. The within-trial noise,  $w(t)$ , is Gaussian-distributed with standard deviation  $\sigma(t)$ :

210

211

$$w(t) \sim N(0, \sigma(t)).$$

212



213

214

Figure 3 Model Schematic. A Components of the model with a transient burst of stimulus-evoked bias and increasing evidence ('BurstIE'), with example traces for the cumulative sum of bias plus evidence, urgency and the resultant motor-level DV traces from a simulated low-value trial. A delay  $T_{ac}$  after stimulus onset,  $t_0$ , the combination of a sudden detection-triggered bias function and growing, noisy sensory evidence began to be accumulated, and with the addition of urgency drove the race between two DVs toward the threshold. The cumulative bias and evidence was half-wave rectified such that (positive) evidence towards the correct (low-value) response was added to the low-value urgency signal, and vice versa. B Alternative evidence and noise functions. For SE models both stepped abruptly to their asymptotic value whereas for IE models both increased according to a gamma function. C Alternative drift-rate bias functions. For 'Burst' models the duration of bias was short, with a maximum of 72 ms, whereas sustained drift-rate bias ('Sust') models had a bias that continued throughout the trial. Waveforms are not drawn to scale.

225

226 Neural Constraints: Based on the principle that neural constraints permit greater model complexity  
 227 without unduly increasing degrees of freedom (O’Connell et al., 2018), from the anticipatory motor  
 228 preparation signals we adopted constraints on not just starting levels (Kelly et al., 2020) but also the  
 229 biased mean urgency buildup rates. The mean Beta starting levels (750 ms post cue) and slopes  
 230 (from 700-800 ms post-cue) were calculated for each regime across participants. To obtain the  
 231 model parameters, we linearly re-scaled the Beta signals within a range from 0, corresponding to  
 232 the lowest starting level, to a fixed bound of 1 corresponding to the Beta threshold—the average  
 233 value of Beta contralateral to the chosen hand across all conditions 50 ms prior to response (see  
 234 Figure 4A). The starting levels and mean rates of urgency buildup for the high and low-value  
 235 alternatives were set to equal the amplitude and temporal slope of the corresponding scaled Beta  
 236 signals for each regime (Table 1).

237 Table 1: EEG-constrained parameters.

Parameter	Symbol	High Coherence	Low Coherence	Interleaved
Starting point contralateral to high value	$Z_c$	.32	.3	.2
Starting point ipsilateral to high value	$Z_i$	.12	.002	0
Mean urgency rate contralateral to high value	$U_c$	1.36	1.09	1.3
Mean urgency rate ipsilateral to high value	$U_i$	1.83	1.7	1.79

238  
 239 Within this neurally-constrained urgency model framework, we fit several alternative bounded  
 240 accumulation models to the data for comparison. It has already been established by several  
 241 researchers that the behavioral patterns in fast value-biased decisions are not well-captured by  
 242 standard accumulation-to-bound models with stationary drift rates (Afacan-Seref et al., 2018;  
 243 Diederich and Busemeyer, 2006; Noorbaloohi et al., 2015). For this reason, we have not compared  
 244 the performance of our neurally-informed models to these standard models (although see Kelly et  
 245 al., (2020) for a comparison between the diffusion decision model and a related neurally-informed  
 246 model). Instead, we restricted our analysis to models that can capture motor preparation  
 247 dynamics—namely the strong empirical signatures of anticipatory urgency—as well as behavior,  
 248 and thus provide a more detailed parsing of multiple biasing phases. With this structure common to  
 249 all models, we explored whether the data were better captured by a stationary (Ratcliff and McKoon,  
 250 2008) or growing (Afacan-Seref et al., 2018; Smith and Lilburn, 2020) evidence function, and by a  
 251 sustained (Afacan-Seref et al., 2018) or transient (Diederich and Busemeyer, 2006) drift-rate bias,  
 252 by comparing four main model variants that featured two plausible alternative ways to implement  
 253 noisy evidence accumulation and two different stimulus-evoked biasing mechanisms:

254 Evidence and noise functions: We compared models with a standard *stationary evidence* (SE)  
 255 function with abrupt onset to *increasing evidence* (IE) models where the evidence and noise  
 256 gradually grow with time (Smith et al., 2014; Smith and Lilburn, 2020) (Figure 3B). Both model types  
 257 had an asymptotic drift rate parameter,  $v$ , to which the mean of the sensory evidence stepped (SE)  
 258 or gradually tended (IE), for each coherence level. A single within-trial noise parameter ( $s$ ) dictated  
 259 the asymptotic standard deviation of Gaussian-distributed within-trial noise. We also estimated an  
 260 onset time for accumulation,  $T_{ac}$ , relative to stimulus onset. In the SE models this parameter  
 261 signalled the onset of the bias accumulation (see below), while the noisy evidence stepped up at a  
 262 later time,  $T_{ev}$ :

$$263 \quad \mu_{SE}(t) = \begin{cases} v & \text{if } t > T_{ev} \\ 0 & \text{otherwise} \end{cases}$$

$$264 \quad \sigma_{SE}(t) = \begin{cases} s & \text{if } t > T_{ev} \\ 0 & \text{otherwise} \end{cases}$$

265 In the IE models, the bias, evidence and noise functions all began at  $T_{ac}$ . The increasing evidence  
 266 and noise functions used were those developed for a time-changed diffusion model (Smith et al.,  
 267 2014; Smith and Lilburn, 2020) in which the drift rate  $v$ , and diffusion coefficient  $s^2$  (the squared

268 standard deviation of the Gaussian-distributed within-trial noise), are both scaled by a growth rate  
269 function  $\vartheta$ :

$$270 \quad \mu_{IE}(t) = v \cdot \vartheta(t)$$

$$271 \quad \sigma_{IE}(t) = s \cdot \sqrt{\vartheta(t)}$$

272 Following Smith and Lilburn (2020, see equation 9),  $\vartheta$  took the form of an incomplete gamma  
273 function with rate  $\beta$ , where the argument  $n$  and  $\beta$  were free parameters:

$$274 \quad \vartheta(t) = \begin{cases} \frac{1}{\Gamma(n)} \int_0^{\beta(t-T_{ac})} e^{-r} r^{n-1} dr, & \text{if } t > T_{ac} \\ 0 & \text{otherwise} \end{cases}$$

275  
276 In this equation  $\Gamma(n)$  is the gamma function. The shape of the function obtained by one of our  
277 model fits is shown in Figure 3B.  
278

279 ***Stimulus-evoked bias functions:*** We also compared two alternative implementations of a drift-rate  
280 bias across different model variants. One featured a sustained drift-rate bias ('Sust') which began at  
281  $T_{ac}$  and lasted until response. The other featured a shorter transient bias, inspired by the apparent  
282 concentrated burst of value-biased activity ('Burst') before evidence accumulation took hold in the  
283 LRP (Figure 3C). Both of these functions involved a bias magnitude parameter ( $v_b$ ) for each regime:

$$284 \quad B_{Sust}(t) = \begin{cases} \pm v_b & \text{if } t \geq T_{ac} \\ 0 & \text{otherwise} \end{cases}$$

$$285 \quad B_{Burst}(t) = \begin{cases} \pm v_b & \text{if } T_{ac} \leq t \leq (T_{ac} + BurstT) \\ 0 & \text{otherwise} \end{cases}$$

286 The bias factor  $\pm v_b$  was positive for high-value trials and negative for low-value trials. The 'Burst'  
287 was composed of a drift-rate bias beginning at  $T_{ac}$  whose duration  $BurstT$  varied on a uniform  
288 distribution from 0-72ms. In preliminary analyses we found that the burst magnitude and its range of  
289 durations could trade off each other such that equivalent fits to behavior could be found for a wide  
290 range of values of the latter. We thus fixed the maximum duration to 72 ms because it produced a  
291 simulated-DV bolus similar in duration to the real LRP (Figure 4 B,C; see Methods). We also  
292 restricted  $T_{ac}$  to a narrow range of 90-100 ms in the fits, close to the apparent onset of the real LRP  
293 bolus; we did not find that expanding this range helped the models to converge.

294 **Model Fits.** Models were fit to the group average of the RT quantiles (see Methods). The  
295 increasing-evidence (IE) models performed better than the stationary-evidence (SE) models, with  
296 the BurstIE model providing the best fit to behavior (Table 2). This model captured all the main  
297 qualitative features of the RT distributions, including the indistinguishable (value-driven) leading  
298 edges of correct high-value and incorrect low-value trials (Figure 4 D-E), and the transition from  
299 value-based to evidence based responses visible in the low-value conditional accuracy functions  
300 (CAFs, Figure 4F). Although the SustIE, BurstSE and SustSE models exhibited a less close  
301 quantitative fit to behavior as reflected in Akaike's Information Criterion (AIC), qualitatively, they all  
302 captured the main behavioral patterns reasonably well including the biased fast guess responses  
303 (Figure 4-Figure Supplements 1-3). The estimated parameters for these four primary models are  
304 given in Table 3.

305 We tested four additional versions of the IE model to assess the contribution of the constrained  
306 urgency and stimulus-evoked bias to the fits (Table 2). First, allowing the urgency rates to be free  
307 parameters, but unbiased by value (Kelly et al., 2020), did not capture the behavior as well as the



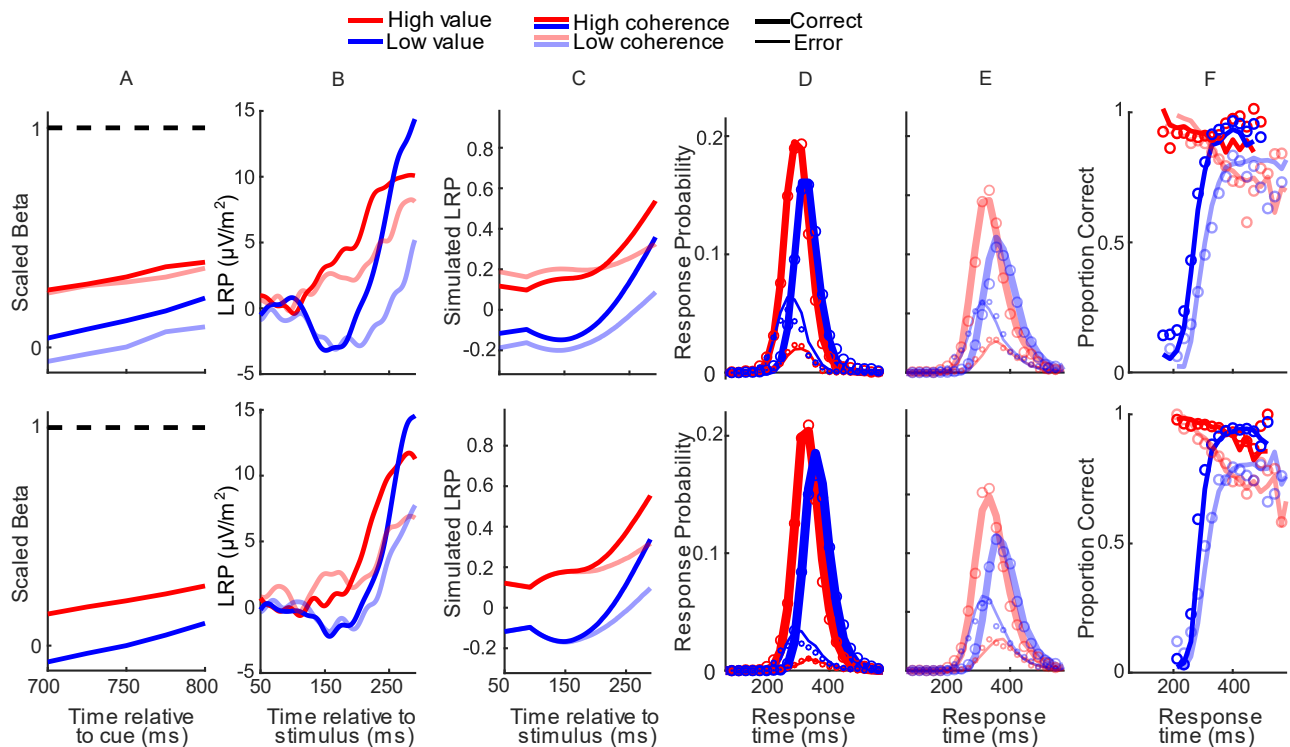
308 constrained IE models. Then, a model with constrained urgency but no stimulus-evoked bias  
 309 produced a far inferior fit. These results suggest that in addition to accounting for the slow temporal  
 310 integration properties of sensory evidence encoding, incorporating both key insights gained from the  
 311 EEG signals was critically important in capturing behavior. We then verified the specific contribution  
 312 of quantitative differences across regimes in the urgency effects measured in the Beta signals by  
 313 showing that swapping the neural constraints across regimes substantially worsened the fit. Finally,  
 314 in Table 2- Table Supplement 1 we report the performance of selected models that incorporate  
 315 additional parameters—such as a ‘drift boost’ under speed pressure and starting-level variability—  
 316 which were included in a neurally-informed model from previous work (Kelly et al., 2020) but had  
 317 little effect here.

318 Table 2. Goodness of fit metrics.

Model	Stimulus-evoked bias	Evidence	k	G <sup>2</sup>	AIC
BurstIE	Burst	Increasing	14	39	67
SustIE	Sustained	Increasing	14	51	79
BurstSE	Burst	Stationary	13	62	88
SustSE	Sustained	Stationary	13	87	113
Unbiased urgency slopes	Burst	Increasing	17	54	88
Urgency-only bias	None	Increasing	11	351	373
Constraints-Swap 1	Burst	Increasing	14	250	278
Constraints-Swap 2	Burst	Increasing	14	111	139

319 Goodness of fit quantified by chi-squared statistic, G<sup>2</sup>. Model comparison was performed using  
 320 Akaike’s Information Criterion (AIC), which penalises for the number of free parameters (k). In the  
 321 two Constraints-Swap models, the constrained parameters for A) high coherence, B) low coherence  
 322 and C) interleaved blocks were taken from the neural signals corresponding to [B,C,A] (Swap 1) and  
 323 [C,A,B] (Swap 2), respectively.

324



325

326 Figure 4: Real and model-simulated waveforms and behavior for blocked session (top row) and  
 327 interleaved session (bottom row). A Scaled Beta signals used to constrain the models. The high

328 versus low-value difference in starting level varied across regime (Regime x Value interaction  
 329  $F(2,32)=4.2$ ,  $p=.03$ , partial  $\eta^2=.87$ ; pairwise comparisons of value-difference indicated low  
 330 coherence blocked > high coherence blocked,  $p=0.01$ ). The Regime x Value interaction for slope  
 331 was not statistically significant ( $F(2,32)=0.29$ ,  $p=.74$ , partial  $\eta^2=.96$ ); B Real LRP. There was a  
 332 significant interaction in bolus amplitude (mean LRP from 150-180 ms) between Value and  
 333 Condition ( $F(3,48)=3.4$ ,  $p=.03$ , partial  $\eta^2=.86$ , but pairwise comparisons of the value difference  
 334 indicated no significant differences between conditions (all  $p>0.15$ ). C Mean simulated trajectories  
 335 of the difference between correct and incorrect DVs from the best-fitting model with Burst drift-rate  
 336 bias and increasing evidence (BurstIE); D-E Real (circles) and model-simulated (solid lines) RT  
 337 distributions. F Real and model-simulated conditional accuracy functions (CAFs). All waveforms  
 338 derived from all trials regardless of accuracy.

339 Table 3: Estimated parameters for the four main models.

Parameter	Symbol	BurstIE	SustIE	BurstSE	SustSE
Asymptotic drift rate (high coherence)	$v_h$	5.8	6.6	4.5	5.0
Asymptotic drift rate (low coherence)	$v_l$	2.6	2.9	2.0	2.2
Drift rate bias (high coherence blocked)	$v_{bh}$	2.3	.54	2.4	0.58
Drift rate bias (low coherence blocked)	$v_{bl}$	2.1	.43	2.3	0.48
Drift rate bias (interleaved)	$v_{bi}$	2.9	.6	3.0	0.66
Within-trial noise asymptotic standard deviation	$s$	1.0	0.95	0.85	0.82
Accumulation onset time (ms)	$T_{ac}$	93	92	99	94
Burst duration range (ms)	$b_{range}$	<b>72</b>	---	<b>72</b>	----
$\vartheta(t)$ – rate	$\beta$	61.7	34.9	---	---
$\vartheta(t)$ – argument	$n$	7.5	6.2	---	---
Evidence onset time (ms)	$T_{ev}$	---	---	210	220
Mean motor time (high coherence blocked) (ms)	$T_{mh}$	81	56	67	60
Mean motor time (low coherence blocked) (ms)	$T_{ml}$	82	50	66	60
Mean motor time (interleaved) (ms)	$T_{mi}$	92	61	77	70
Urgency rate variability	$S_u$	0.43	0.39	0.38	0.42
Motor time variability (ms)	$S_t$	57	53	77	86

340 Note: Fixed parameter shown in bold typeface.

341 **Decision Variable Simulations.** We qualitatively explored the correspondence between the fast  
 342 neural dynamics of the LRP and simulated decision process by plotting the difference between the  
 343 two DVs (Figure 4 B-C). The starting levels are not comparable because, unlike the simulated  
 344 process, the real LRP was baseline corrected, and the initially decreasing value bias in the  
 345 simulated waveforms is not seen in the LRP due to interfering posterior slow potentials (see Figure  
 346 2-Figure Supplement 1). There was, however, good correspondence between the dynamics from  
 347 the onset of the deflection, which was notably absent in the alternative SustIE and SustSE model  
 348 simulations (Figure 4-Figure Supplements 1,3). The BurstIE model effectively captured aspects of  
 349 both EEG motor preparation signatures through its distinct countervailing biasing mechanisms.

## 350 Discussion

351 Convergent evidence from motor preparation signals and behavioral modeling demonstrated that a  
 352 dynamic sequence of opposing value biases and non-stationary evidence accumulation all played  
 353 important roles in forming the rapid, multiphasic decisions on this task. In most decision-making  
 354 models a “starting-point bias” parameter—shifting the starting point of accumulation—treats  
 355 anticipatory biases as static adjustments before the process begins (Leite and Ratcliff, 2011; Mulder  
 356 et al., 2012). Here, far from creating a stable starting point to kick off a stationary decision process,  
 357 we found a dynamic pattern of biased motor preparation that is best understood as a two-  
 358 dimensional race beginning well in advance of the stimulus. Constraining a behavioral model with

359 these signals enabled us to characterise a surprisingly complex process, revealing biasing  
360 mechanisms that would otherwise have been inaccessible.

361 In agreement with previous research that has called for nonstationary accounts of value biasing in  
362 time-pressured decisions (Diederich and Busemeyer, 2006), we found that the value bias was  
363 largely concentrated in the early part of the process. The particular dynamics of the RDK stimulus,  
364 featuring a substantial lag between stimulus onset and the emergence of discriminatory sensory  
365 evidence, may have provided a focal point for the bias to be expressed separately from the  
366 evidence itself. However, the signature expressions of this sequential detection-discrimination  
367 effect—namely, the almost purely value-driven nature of both the leading edge of RT distributions  
368 and of the initial stimulus-evoked LRP deflection—are observed also for discriminations of stimulus  
369 displacement (Noorbaloochi et al., 2015) and color (Afacan-Seref et al., 2018), suggesting the  
370 phenomenon generalises beyond the RDK stimulus. While our findings indicate that a strong  
371 transient drift-rate bias better captures the data relative to a sustained, constant bias, the possibility  
372 of a hybrid of the two, where the initial detection-triggered burst reduces to a smaller sustained bias,  
373 was not tested because it was assumed to go beyond a reasonable number of free parameters.  
374 Thus, uncertainty remains regarding the exact temporal profile of this stimulus-evoked bias, and we  
375 cannot say that it fully disappears beyond the burst.

376 The implication of a negative “drift-rate” bias in urgency is counterintuitive but not completely without  
377 precedent. In the context of the diffusion decision model with unequal prior probabilities, Moran  
378 (2015) found that a negative drift-rate bias featured alongside a starting point bias in the optimal  
379 decision strategy under certain assumed bound settings, albeit not when bound settings were  
380 assumed controllable as part of the optimization calculation. Here, a similar tradeoff between the  
381 positive starting-level bias and negative urgency-rate bias may have arisen from the fact that the  
382 greater the starting point bias, the greater the need for a steeper low-value urgency signal to give it  
383 a chance to overtake the high-value signal when the low-value DV represents the correct response.

384 Understanding the processes generating the behaviors in this task rested on the neurophysiological  
385 identification of strategic urgency biases. The anticipatory nature of the early Beta signal buildup  
386 aided in specifically linking it to evidence-independent urgency, and its incorporation in the model  
387 was key to understanding the subsequent processing of the motion stimulus. The most significant  
388 disadvantage of relying on group-average neurophysiology to constrain our model, however, was  
389 that we were unable to examine individual differences in behavior. The extent to which these  
390 different forms of bias might trade off each other at the individual level remains for now an open  
391 question. Nevertheless, the finding of a negative urgency rate bias as part of the participants’  
392 dominant strategy highlights the broad range of dynamic adjustments that can be made in the  
393 course of fast-paced sensorimotor decisions.

## 394 Methods

395 **Participants.** The experiment involved one psychophysical training session and two EEG recording  
396 sessions. As the task was challenging, the training session served a dual purpose of giving  
397 participants the time to learn the task and to screen out those who found it too difficult. Twenty-nine  
398 adult human participants performed the training session. Eleven discontinued who either did not  
399 sufficiently improve to the point of being able to perform the task well, or chose to do so due to  
400 having other commitments. Eighteen participants (8 female) thus completed the two EEG sessions.  
401 Motor preparation biasing effects tend to be consistent and robust (e.g. effect sizes of at least  $d=1$   
402 for similar “bolus” effects in Afacan-Seref et al., 2018), and 15-18 participants provide 80% power to  
403 detect medium-to-large effect sizes. Participants all had normal or corrected-to-normal vision. They  
404 each provided informed, written consent to the procedures, which were approved by the Ethics  
405 Committee of the School of Psychology at Trinity College Dublin, and the Human Research Ethics  
406 Committee for the Sciences, at University College Dublin. Participants were compensated with €20  
407 for the training session and €32 for their participation in each EEG session with the potential to earn

408 up to €12 further depending on their performance. One of the participants was an author and the  
409 remainder were naive.

410 **Setup.** Participants were seated in a dark booth, with their heads stabilized in a chin rest placed 57  
411 cm from a cathode ray tube monitor (frame rate 75 Hz, resolution 1024 × 768) with a black  
412 background. They rested their left/right thumbs on the left/right buttons of a symmetric computer  
413 mouse secured to the table in front of them.

414 **Task.** The task was programmed in Psychtoolbox for MATLAB (Brainard, 1997). Trials began with  
415 the presentation of a central grey 0.25° fixation square. Upon achieving fixation (4° radius detection  
416 window, EyeLink 1000, SR Research), a value cue replaced the fixation square after either 400 or  
417 450 ms (randomly selected) and remained on screen, until the end of the trial (Figure 1). The cue  
418 consisted of equiluminant green and cyan arrows placed and pointing to the left and right of center,  
419 indicating the directions that would be worth 30 points (high value) or 10 points (low value) if  
420 subsequently presented and correctly responded to with the corresponding hand within the  
421 deadline. Incorrect or late responses were worth 0 points. Color-value assignment was randomly  
422 counterbalanced across participants. The RDK stimulus (5° diameter) appeared and commenced  
423 moving either 850 or 900 ms (randomly selected) after cue onset and lasted 600 or 781 ms for the  
424 shorter or longer deadline conditions, respectively. Participants were required to maintain fixation  
425 throughout, and upon stimulus offset received feedback on whether they were 'Correct!',  
426 'WRONG!', 'TOO SLOW!' or 'TOO EARLY! WAIT FOR CUE ...' and on the total points, and the  
427 number of points missed for each trial type (blue and green), at the end of each block.

428 The task was performed in three blocked regimes: High coherence (51.2%) with a short deadline  
429 (365 ms); low coherence (19.2%) with a slightly longer deadline (475 ms); and interleaved high and  
430 low coherence with the longer deadline. The RDK stimulus was adapted from code from the  
431 Shadlen laboratory (Gold and Shadlen, 2003; Roitman and Shadlen, 2002). A set of white dots were  
432 presented within a circular aperture of 5° in diameter that was the same black color as the  
433 background. The dot density was 16.7 dots per °s. One third of the total number of dots was visible  
434 on screen at any one time; each dot remained on screen for one 13.3-ms frame and was replotted 2  
435 frames later as the 3 sets of dots were alternated. Depending on the coherence level, each dot had  
436 either a 19.2% or 51.2% chance of being replotted by an offset in the direction of coherent motion at  
437 a rate of 5°/s. Otherwise the dots were randomly relocated within the aperture. The first onset of  
438 coherent motion thus occurred 40 ms (3 frames) after the onset of the stimulus. If an offset dot was  
439 set to be plotted outside of the aperture, it was replotted in a random location on the edge of the  
440 aperture opposite to the direction of motion.

441 **Procedure.** So that participants could become familiar with the task, and particularly get used to its  
442 fast pace, they performed one session of psychophysical training before the main experimental  
443 sessions. Blocks in the training sessions comprised 80 trials. The session began with blocks of high-  
444 coherence trials with a long deadline and without value bias (20 points for each direction; both arrow  
445 cues were yellow). The deadline was gradually reduced to 365 ms. The same procedure was then  
446 followed for low-coherence blocks. If participants had great difficulty with the low coherence, the  
447 experimenter gave them some further practice starting at 45% and gradually brought it down to  
448 19.2%. Finally, participants practiced an equal number of biased blocks in the high-coherence, low-  
449 coherence, and interleaved high- and low-coherence regimes.

450  
451 Participants performed the two blocked regimes (5 or 6 blocks each of 120 trials) in one EEG  
452 recording session and the interleaved regime (10 or 12 blocks) in the other. Due to experimenter  
453 error, one participant performed the blocked experimental session twice and we included the data  
454 from both sessions in our analyses. The blocks within each regime were run consecutively to ensure  
455 that subjects would settle into a strategy, and the order of regimes and sessions was randomized. In  
456 training and throughout the EEG recording sessions, participants were encouraged to adopt a  
457 strategy that would maximise their points and were informed that the points earned in two randomly  
458 selected blocks (one per regime in the blocked session) would determine their bonus payment in



459 each recording session. Participants were provided with the total number of points earned at the  
460 end of the block as well as the number of points missed in the block for each trial type (blue and  
461 green), to motivate them and help them determine whether they were biasing too much or too little.  
462 The experimenters helped participants interpret this feedback and when needed provided frequent  
463 reminders that it was important to pay attention to both the value cue and the stimulus and that  
464 there were no points awarded for late responses.

465  
466 **Behavioral analyses.** RTs were measured relative to the onset of the RDK stimulus. RTs less than  
467 50 ms (0.23% of trials) were excluded from behavioral analyses and model fitting. Responses up to  
468 and beyond the deadline were included in all analyses so long as they occurred before the end of  
469 the RDK stimulus; trials without a response (0.21% of trials) were excluded. One participant was an  
470 outlier in terms of biasing (error rate difference between low-value and high-value trials fell more  
471 than two interquartile ranges above the upper quartile) and was excluded from further analyses.

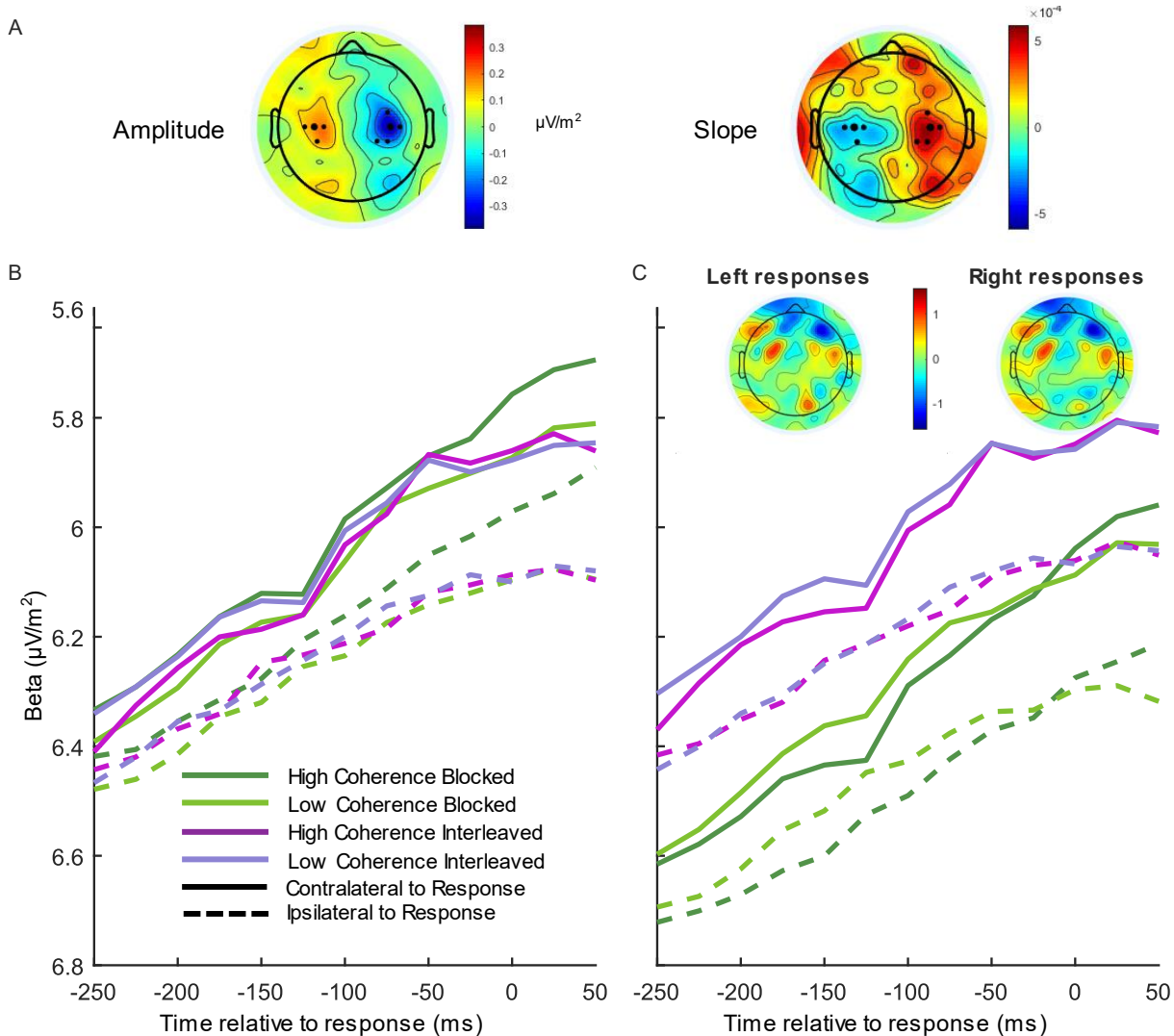
472  
473 **Electrophysiological data analysis.** Continuous EEG data from 128 scalp electrodes were  
474 acquired using an ActiveTwo system (BioSemi, The Netherlands) and digitized at 1024 Hz. Offline  
475 analyses were performed using in-house MATLAB scripts (MathWorks, Natick, MA) using data  
476 reading, channel interpolation and topographic plot functions from the EEGLAB toolbox (Delorme  
477 and Makeig, 2004). EEG data were low-pass filtered by convolution with a 137-tap hanning-  
478 windowed sinc function designed to provide a 3-dB corner frequency of 37 Hz with strong  
479 attenuation at the mains frequency (50 Hz), detrended and average referenced. The data were  
480 epoched from -150 to 2450 ms relative to the cue onset. We identified and interpolated (spherical  
481 splines) channels with excessively high variance with respect to neighboring channels and channels  
482 that saturated or flat-lined during a given block. Trials were rejected upon detection of artifacts  
483 between cue and response (on selected frontal channels sensitive to blinks with magnitude  $> 70\mu\text{V}$ ,  
484 or  $50\mu\text{V}$  for the selected motor channels used in our analyses). Then, to mitigate the effects of  
485 volume conduction across the scalp, current source density (CSD) transformation was applied to the  
486 single-trial epochs (Kayser and Tenke, 2006; Kelly and O'Connell, 2013). Shorter cue-locked (-150  
487 to 1500ms), stimulus-locked (-1000 to 650ms) and response-locked (-400 to 210ms) event-related  
488 potentials (ERPs) were then extracted from the longer epochs, and baseline corrected to the 100-  
489 ms window following the cue. The LRP was calculated as the difference in ERP between electrodes  
490 at standard 10-20 sites C3 and C4 (Gratton et al., 1988), by subtracting the ERP ipsilateral to the  
491 correct response from the contralateral ERP.

492  
493 Beta-band activity was measured using a short-time Fourier transform applied to 300-ms windows  
494 stepped by 25 ms at a time, and by taking the mean amplitude in the range 14-30 Hz. We restricted  
495 our measurements to the Beta band as opposed to including both Mu and Beta (Kelly et al., 2020)  
496 to avoid any potential interference from posterior Alpha-band activity which is known to lateralise in  
497 situations where attention can be guided to the left or right. We found posterior lateralization to be  
498 minimal in the Beta-band amplitude, and while there was an appreciable slope difference this was  
499 clearly separated from the motor-related areas (see Figure 5A). To ensure precise measurements  
500 for model constraints, Beta was measured from electrodes selected per individual based on  
501 exhibiting the strongest decrease at response relative to cue or stimulus onset. Standard sites  
502 C3/C4 were selected by default where difference-topography foci were close and symmetric (9 of 17  
503 subjects), and otherwise electrodes were selected among those proximal to the foci based on their  
504 exhibiting smooth decline in their amplitude timecourses from cue to response. Where uncertain,  
505 preference was given to symmetry across hemispheres and electrodes that reached a common  
506 threshold across conditions at response.

507  
508 For these individually-selected electrodes (marked in Figure 5A), the contralateral beta just prior to  
509 response (-50ms) reached a threshold across conditions (Figure 5B; the error bars in Figure 2C  
510 break this down further into value and response conditions). The ipsilateral Beta diverged between  
511 the blocked high coherence and the other conditions, indicating a closer race for the most speed-  
512 pressured condition. When the standard C3/C4 sites were instead selected, however, we found an  
513 offset between the blocked conditions and the interleaved conditions (Figure 5C). This was



514 unexpected, but not entirely surprising due to the fact that the blocked and interleaved sessions  
515 were performed on different days for all participants, and the different demands potentially resulted  
516 in some global changes in measured Beta amplitude not directly related to motor preparation. The  
517 inset topographies show the overall difference in Beta amplitude between the two sessions at  
518 response; the difference does not appear to be of motor origin. As this difference was evident to a  
519 similar degree before the stimulus onset, we recalculated the Beta starting points and slopes with  
520 the C3/C4 electrodes after first subtracting the offset between the two sessions at -50ms from  
521 response from all Beta traces. We found that the calculated neural constraints were similar  
522 regardless of electrode choice (Figure 5-Supplementary Table 1). The starting levels were almost  
523 identical except for a small difference in the low-coherence-blocked levels both contralateral and  
524 ipsilateral to high value. The steeper ipsilateral slope was also maintained and the difference  
525 relative to contralateral slope had a similar magnitude. Due to our desire to obtain the clearest view  
526 of motor activity possible, we used the individually-selected electrodes in our modeling and  
527 analyses.  
528



529  
530

531 Figure 5 Electrode selection for Beta analysis. A Topographies of the difference between left- and  
532 right-cued trials for Beta amplitude at 750 ms relative to amplitude at the cue, and slope from 700-  
533 800 ms after the cue. Standard sites C3/C4 are marked with large black dots, while other electrodes  
534 that were selected for certain individuals are marked with smaller dots. B Response-locked Beta  
535 contralateral (solid) and ipsilateral (dashed) to response for the four conditions with individually  
536 selected electrodes. C Same as B, but with standard sites C3/C4 selected for all participants.

537 Topographies show the average difference in Beta amplitude between blocked and interleaved  
538 conditions at -50ms relative to response, for right and left responses separately.

539

540 **Statistical Approach.** Repeated measures ANOVAs with both Value and Regime/Conditions  
541 included as appropriate, were used to test for differences in behavioral and neural amplitude and  
542 slope measures, and followed up with pairwise, FDR-corrected t-tests. Given the study's focus on  
543 mechanisms common to the various conditions, we state main effects of value in the main text, and  
544 address regime effects in the figure legends. The onsets for the Beta signals were calculated using  
545 a jackknife procedure in which the traces were computed for the average signals of 16 subjects at a  
546 time, with each subject systematically excluded in turn, to compute the first time at which it  
547 exceeded 20% of the response threshold for that subgroup. The standard errors of each condition  
548 were then scaled up by 16 and a repeated-measures ANOVA was conducted.

549

550 **Modeling.** We fit each model to 16 RT distributions (Figure 4 D-E): correct and error responses for  
551 high- and low-value trials across the four conditions. We partitioned each distribution into 6 bins  
552 bounded by the 0.1, 0.3, 0.5, 0.7 and 0.9 quantiles. Models were fit by minimising the chi-squared  
553 statistic  $G^2$ , between the real quantiles and those obtained from Monte-Carlo simulated RT  
554 distributions:

$$555 \quad G^2 = 2 \left( \sum_{c=1}^4 \sum_{v=1}^2 N_{c,v} \left[ \sum_{o=1}^2 \sum_{q=1}^6 p_{c,v,o,q} \log \frac{p_{c,v,o,q}}{\pi_{c,v,o,q}} \right] \right)$$

556 where  $p_{c,v,o,q}$  and  $\pi_{c,v,o,q}$  are the observed and predicted proportions of responses in bin  $q$ ,  
557 bounded by the quantiles, of outcome  $o$  (correct/error) of condition  $c$  (coherence x  
558 Blocked/Interleaved) and value  $v$  (high/low), respectively.  $N_{c,v}$  is the number of valid trials per  
559 condition and value.

560 In the model simulations the urgency signals were defined to equal their scaled (750 ms post-cue)  
561 Beta levels at 100 ms prior to stimulus onset time. In the experiment, stimulus onset corresponded  
562 to 850 or 900 ms post cue; thus, we started the stimulus-evoked accumulation with a 50-ms delay  
563 on half of the trials and adjusted the RTs accordingly. For the IE models, the shape function  $\vartheta(t)$   
564 was obtained in our simulations by numerical integration. We searched the parameter space using  
565 the particle swarm optimization algorithm (Kennedy and Eberhart, 1995) as implemented in  
566 MATLAB, initialized with a number of swarms equal to 10 times the number of parameters to be  
567 estimated. To aid convergence we set the same random seed for each simulation within a search,  
568 which comprised 20,000 trials per value per condition. Because there was randomness associated  
569 with the optimization we ran it at least 3 times for each model. We followed this with a call to  
570 `fminsearchbnd` (Nelder and Mead, 1965) initialized with each of the parameter estimates for the  
571 model and any nested models, to obtain a second set of parameter estimates. We then obtained a  
572 final  $G^2$  for each parameter vector by running a simulation with 2,000,000 trials and initialized with a  
573 different seed, and selected that with the lowest value. We performed model comparison using AIC,  
574 which penalises models for complexity:

$$575 \quad AIC = G^2 + 2k$$

576 where  $k$  is the number of free parameters. The simulated decision variables for comparison with the  
577 real LRP were obtained by subtracting the average decision variable of the incorrect option from the  
578 correct option, time-locked to stimulus onset. We did not make the simulations fall back to zero upon  
579 bound crossing, and so the signals continue to build and become less comparable to the real  
580 average LRP once it peaks and falls due to responses being made. Initially we had allowed the  
581 possible range of burst durations to be a free parameter in the BurstIE model and obtained several  
582 equally good fits in which this parameter was spread over a wide range of values, trading off with  
583 the bias magnitude. We thus decided to constrain this parameter to correspond to the real LRP as  
584 closely as possible, with the understanding that within our framework we could not be certain of its

585 exact form. We fit the model four times with the burst duration range set to 30, 50, 70 and 90 ms,  
586 and compared the time between burst onset and the low-value turnaround in the real LRP (53.7 ms)  
587 to those in the simulations. Finding the 70-ms duration range gave the closest match (52 ms), we  
588 then adjusted the duration-range parameter holding all others constant to obtain a 54-ms simulated  
589 LRP duration when the range parameter was set to 72 ms. We adopted this value in all further fits to  
590 the BurstIE and BurstSE models.

## 591 Acknowledgements

592 The authors thank Louisa Spence for data collection. This study was funded by the European  
593 Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant  
594 agreement No 842143, the European Research Council Starting Grant No 63829, the European  
595 Research Council Consolidator Grant IndDecision – 865474, the Irish Research Council  
596 (GOIPD/2017/1261), and by Science Foundation Ireland Grant No 15/CDA/3591. Most of the model  
597 fitting was performed on the Lonsdale cluster which is funded through grants from Science  
598 Foundation Ireland and maintained by the Trinity Centre for High Performance Computing  
599 (Research IT, Trinity College Dublin).

## 600 Competing Interests

601 The authors report no competing interests.

602

## 603 References

- 604 Afacan-Seref, K., Steinemann, N.A., Blangero, A., Kelly, S.P., 2018. Dynamic Interplay of Value and Sensory  
605 Information in High-Speed Decision Making. *Current Biology* 28, 795-802.e6.  
606 <https://doi.org/10.1016/j.cub.2018.01.071>
- 607 Brainard, D.H., 1997. The psychophysics toolbox. *Spatial vision* 10, 433–436.
- 608 Brown, S.D., Heathcote, A., 2008. The simplest complete model of choice response time: Linear ballistic  
609 accumulation. *Cognitive psychology* 57, 153–178. <https://doi.org/10.1016/j.cogpsych.2007.12.002>
- 610 Churchland, A.K., Kiani, R., Shadlen, M.N., 2008. Decision-making with multiple alternatives. *Nature*  
611 *neuroscience* 11, 693–702. <https://doi.org/10.1038/nn.2123>
- 612 Cisek, P., Puskas, G.A., El-Murr, S., 2009. Decisions in changing conditions: the urgency-gating model. *Journal*  
613 *of Neuroscience* 29, 11560–11571. <https://doi.org/10.1523/JNEUROSCI.1844-09.2009>
- 614 de Lange, F.P., Rahnev, D.A., Donner, T.H., Lau, H., 2013. Prestimulus oscillatory activity over motor cortex  
615 reflects perceptual expectations. *Journal of Neuroscience* 33, 1400–1410.  
616 <https://doi.org/10.1523/JNEUROSCI.1094-12.2013>
- 617 Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics  
618 including independent component analysis. *Journal of neuroscience methods* 134, 9–21.  
619 <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- 620 Diederich, A., Busemeyer, J.R., 2006. Modeling the effects of payoff on response bias in a perceptual  
621 discrimination task: Bound-change, drift-rate-change, or two-stage-processing hypothesis.  
622 *Perception & Psychophysics* 68, 194–207. <https://doi.org/10.3758/BF03193669>
- 623 Ditterich, J., 2006. Evidence for time-variant decision making. *European Journal of Neuroscience* 24, 3628–  
624 3641. <https://doi.org/10.1111/j.1460-9568.2006.05221.x>
- 625 Donner, T.H., Siegel, M., Fries, P., Engel, A.K., 2009. Buildup of choice-predictive activity in human motor  
626 cortex during perceptual decision making. *Current Biology* 19, 1581–1585.  
627 <https://doi.org/10.1016/j.cub.2009.07.066>

- 628 Evans, N.J., Hawkins, G.E., Boehm, U., Wagenmakers, E.-J., Brown, S.D., 2017. The computations that support  
629 simple decision-making: A comparison between the diffusion and urgency-gating models. *Scientific*  
630 *reports* 7, 1–13. <https://doi.org/10.1038/s41598-017-16694-7>
- 631 Feng, S., Holmes, P., Rorie, A., Newsome, W.T., 2009. Can monkeys choose optimally when faced with noisy  
632 stimuli and unequal rewards? *PLoS computational biology* 5, e1000284.  
633 <https://doi.org/10.1371/journal.pcbi.1000284>
- 634 Feuerriegel, D., Jiwa, M., Turner, W.F., Andrejević, M., Hester, R., Bode, S., 2019. Tracking dynamic  
635 adjustments to decision making and performance monitoring processes in conflict tasks. *BioRxiv*.  
636 <https://doi.org/10.1101/2019.12.19.883447>
- 637 Gluth, S., Rieskamp, J., Büchel, C., 2013. Classic EEG motor potentials track the emergence of value-based  
638 decisions. *NeuroImage* 79, 394–403. <https://doi.org/10.1016/j.neuroimage.2013.05.005>
- 639 Gold, J.I., Shadlen, M.N., 2003. The influence of behavioral context on the representation of a perceptual  
640 decision in developing oculomotor commands. *Journal of Neuroscience* 23, 632–651.  
641 <https://doi.org/10.1523/JNEUROSCI.23-02-00632.2003>
- 642 Gratton, G., Coles, M.G., Sirevaag, E.J., Eriksen, C.W., Donchin, E., 1988. Pre-and poststimulus activation of  
643 response channels: a psychophysiological analysis. *Journal of Experimental Psychology: Human*  
644 *perception and performance* 14, 331. <https://doi.org/10.1037/0096-1523.14.3.331>
- 645 Hanks, T., Kiani, R., Shadlen, M.N., 2014. A neural mechanism of speed-accuracy tradeoff in macaque area  
646 LIP. *Elife* 3, e02260. <https://doi.org/10.7554/eLife.02260>
- 647 Hanks, T.D., Mazurek, M.E., Kiani, R., Hopp, E., Shadlen, M.N., 2011. Elapsed decision time affects the  
648 weighting of prior probability in a perceptual decision task. *Journal of Neuroscience* 31, 6339–6352.  
649 <https://doi.org/10.1523/JNEUROSCI.5613-10.2011>
- 650 Kayser, J., Tenke, C.E., 2006. Principal components analysis of Laplacian waveforms as a generic method for  
651 identifying ERP generator patterns: I. Evaluation with auditory oddball tasks. *Clinical*  
652 *neurophysiology* 117, 348–368. <https://doi.org/10.1016/j.clinph.2005.08.034>
- 653 Kelly, S.P., Corbett, E.A., O’Connell, R.G., 2020. Neurocomputational mechanisms of prior-informed  
654 perceptual decision-making in humans. *Nature Human Behaviour* 1–15.  
655 <https://doi.org/10.1038/s41562-020-00967-9>
- 656 Kelly, S.P., O’Connell, R.G., 2013. Internal and external influences on the rate of sensory evidence  
657 accumulation in the human brain. *The Journal of Neuroscience* 33, 19434–19441.  
658 <https://doi.org/10.1523/JNEUROSCI.3355-13.2013>
- 659 Kennedy, J., Eberhart, R., 1995. Particle swarm optimization, in: *Proceedings of the IEEE International*  
660 *Conference on Neural Networks*. IEEE, Perth, Australia, pp. 1942–1948.
- 661 Leite, F.P., Ratcliff, R., 2011. What cognitive processes drive response biases? A diffusion model analysis.  
662 *Judgment & Decision Making* 6.
- 663 Link, S.W., Heath, R.A., 1975. A sequential theory of psychological discrimination. *Psychometrika* 40, 77–105.
- 664 Moran, R., 2015. Optimal decision making in heterogeneous and biased environments. *Psychonomic bulletin*  
665 *& review* 22, 38–53. <https://doi.org/10.3758/s13423-014-0669-3>
- 666 Mulder, M.J., Wagenmakers, E.-J., Ratcliff, R., Boekel, W., Forstmann, B.U., 2012. Bias in the brain: a diffusion  
667 model analysis of prior probability and potential payoff. *The Journal of Neuroscience* 32, 2335–2343.  
668 <https://doi.org/10.1523/JNEUROSCI.4156-11.2012>
- 669 Murphy, P.R., Boonstra, E., Nieuwenhuis, S., 2016. Global gain modulation generates time-dependent  
670 urgency during perceptual choice in humans. *Nature communications* 7, 13526.  
671 <https://doi.org/10.1038/ncomms13526>
- 672 Nelder, J.A., Mead, R., 1965. A simplex method for function minimization. *The computer journal* 7, 308–313.  
673 <https://doi.org/10.1093/comjnl/7.4.308>
- 674 Noorbalooci, S., Sharon, D., McClelland, J.L., 2015. Payoff information biases a fast guess process in  
675 perceptual decision making under deadline pressure: evidence from behavior, evoked potentials,  
676 and quantitative model comparison. *Journal of Neuroscience* 35, 10989–11011.  
677 <https://doi.org/10.1523/JNEUROSCI.0017-15.2015>



- 678 O'Connell, R.G., Dockree, P.M., Kelly, S.P., 2012. A supramodal accumulation-to-bound signal that  
679 determines perceptual decisions in humans. *Nature neuroscience* 15, 1729–1735.  
680 <https://doi.org/10.1038/nn.3248>
- 681 O'Connell, R.G., Shadlen, M.N., Wong-Lin, K., Kelly, S.P., 2018. Bridging Neural and Computational  
682 Viewpoints on Perceptual Decision-Making. *Trends in Neurosciences* 41, 838–852.  
683 <https://doi.org/10.1016/j.tins.2018.06.005>
- 684 Ratcliff, R., 1978. A theory of memory retrieval. *Psychological review* 85, 59. <https://doi.org/10.1037/0033-295X.85.2.59>
- 685
- 686 Ratcliff, R., McKoon, G., 2008. The diffusion decision model: theory and data for two-choice decision tasks.  
687 *Neural computation* 20, 873–922. <https://doi.org/10.1162/neco.2008.12-06-420>
- 688 Rinkenauer, G., Osman, A., Ulrich, R., Müller-Gethmann, H., Mattes, S., 2004. On the locus of speed-accuracy  
689 trade-off in reaction time: inferences from the lateralized readiness potential. *Journal of*  
690 *Experimental Psychology: General* 133, 261. <https://doi.org/10.1037/0096-3445.133.2.261>
- 691 Roitman, J.D., Shadlen, M.N., 2002. Response of neurons in the lateral intraparietal area during a combined  
692 visual discrimination reaction time task. *Journal of neuroscience* 22, 9475–9489.  
693 <https://doi.org/10.1523/JNEUROSCI.22-21-09475.2002>
- 694 Rorie, A.E., Gao, J., McClelland, J.L., Newsome, W.T., 2010. Integration of sensory and reward information  
695 during perceptual decision-making in lateral intraparietal cortex (LIP) of the macaque monkey. *PloS*  
696 *one* 5, e9308. <https://doi.org/10.1371/journal.pone.0009308>
- 697 Shinn, M., Ehrlich, D.B., Lee, D., Murray, J.D., Seo, H., 2020. Confluence of timing and reward biases in  
698 perceptual decision-making dynamics. *Journal of Neuroscience* 40, 7326–7342.  
699 <https://doi.org/10.1523/JNEUROSCI.0544-20.2020>
- 700 Simen, P., Contreras, D., Buck, C., Hu, P., Holmes, P., Cohen, J.D., 2009. Reward rate optimization in two-  
701 alternative decision making: empirical tests of theoretical predictions. *Journal of Experimental*  
702 *Psychology: Human Perception and Performance* 35, 1865. <https://doi.org/10.1037/a0016926>
- 703 Smith, P.L., Lilburn, S.D., 2020. Vision for the blind: visual psychophysics and blinded inference for decision  
704 models. *Psychonomic Bulletin & Review*. <https://doi.org/10.3758/s13423-020-01742-7>
- 705 Smith, P.L., Ratcliff, R., 2009. An integrated theory of attention and decision making in visual signal  
706 detection. *Psychological review* 116, 283. <https://doi.org/10.1037/a0015156>
- 707 Smith, P.L., Ratcliff, R., 2004. Psychology and neurobiology of simple decisions. *Trends in neurosciences* 27,  
708 161–168. <https://doi.org/10.1016/j.tins.2004.01.006>
- 709 Smith, P.L., Ratcliff, R., Sewell, D.K., 2014. Modeling perceptual discrimination in dynamic noise: Time-  
710 changed diffusion and release from inhibition. *Journal of Mathematical Psychology* 59, 95–113.  
711 <https://doi.org/10.1016/j.jmp.2013.05.007>
- 712 Standage, D., You, H., Wang, D., Dorris, M.C., 2011. Gain modulation by an urgency signal controls the  
713 speed–accuracy trade-off in a network model of a cortical decision circuit. *Frontiers in*  
714 *computational neuroscience* 5, 7. <https://doi.org/10.3389/fncom.2011.00007>
- 715 Stanford, T.R., Shankar, S., Massoglia, D.P., Costello, M.G., Salinas, E., 2010. Perceptual decision making in  
716 less than 30 milliseconds. *Nature neuroscience* 13, 379. <https://doi.org/10.1038/nn.2485>
- 717 Steinemann, N.A., O'Connell, R.G., Kelly, S.P., 2018. Decisions are expedited through multiple neural  
718 adjustments spanning the sensorimotor hierarchy. *Nature communications* 9, 1–13.  
719 <https://doi.org/10.1038/s41467-018-06117-0>
- 720 Summerfield, C., Koechlin, E., 2010. Economic Value Biases Uncertain Perceptual Choices in the Parietal and  
721 Prefrontal Cortices. *Front. Hum. Neurosci.* 4. <https://doi.org/10.3389/fnhum.2010.00208>
- 722 Thura, D., Beaugregard-Racine, J., Fradet, C.-W., Cisek, P., 2012. Decision making by urgency gating: theory  
723 and experimental support. *Journal of neurophysiology* 108, 2912–2930.  
724 <https://doi.org/10.1152/jn.01071.2011>
- 725 Thura, D., Cisek, P., 2014. Deliberation and Commitment in the Premotor and Primary Motor Cortex during  
726 Dynamic Decision Making. *Neuron* 81, 1401–1416. <https://doi.org/10.1016/j.neuron.2014.01.031>
- 727 Urai, A.E., De Gee, J.W., Tsetsos, K., Donner, T.H., 2019. Choice history biases subsequent evidence  
728 accumulation. *Elife* 8, e46331. <https://doi.org/https://doi.org/10.7554/eLife.46331>



- 729 Usher, M., McClelland, J.L., 2001. The time course of perceptual choice: the leaky, competing accumulator  
730 model. *Psychological review* 108, 550. <https://doi.org/10.1037/0033-295X.108.3.550>
- 731 Van Vugt, M.K., Simen, P., Nystrom, L., Holmes, P., Cohen, J.D., 2014. Lateralized readiness potentials reveal  
732 properties of a neural mechanism for implementing a decision threshold. *PloS one* 9, e90943.  
733 <https://doi.org/10.1371/journal.pone.0090943>
- 734 Voss, A., Rothermund, K., Voss, J., 2004. Interpreting the parameters of the diffusion model: An empirical  
735 validation. *Memory & cognition* 32, 1206–1220. <https://doi.org/10.3758/BF03196893>
- 736 Weindel, G., Anders, R., Alario, F.-X., Burle, B., in press. Assessing model-based inferences in decision making  
737 with single-trial response time decomposition. *Journal of Experimental Psychology: General*.  
738 <https://hal.archives-ouvertes.fr/hal-03006342>
- 739 White, C.N., Poldrack, R.A., 2014. Decomposing bias in different types of simple decisions. *Journal of*  
740 *Experimental Psychology: Learning, Memory, and Cognition* 40, 385.  
741 <https://doi.org/10.1037/a0034851>

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## Figure and table supplements

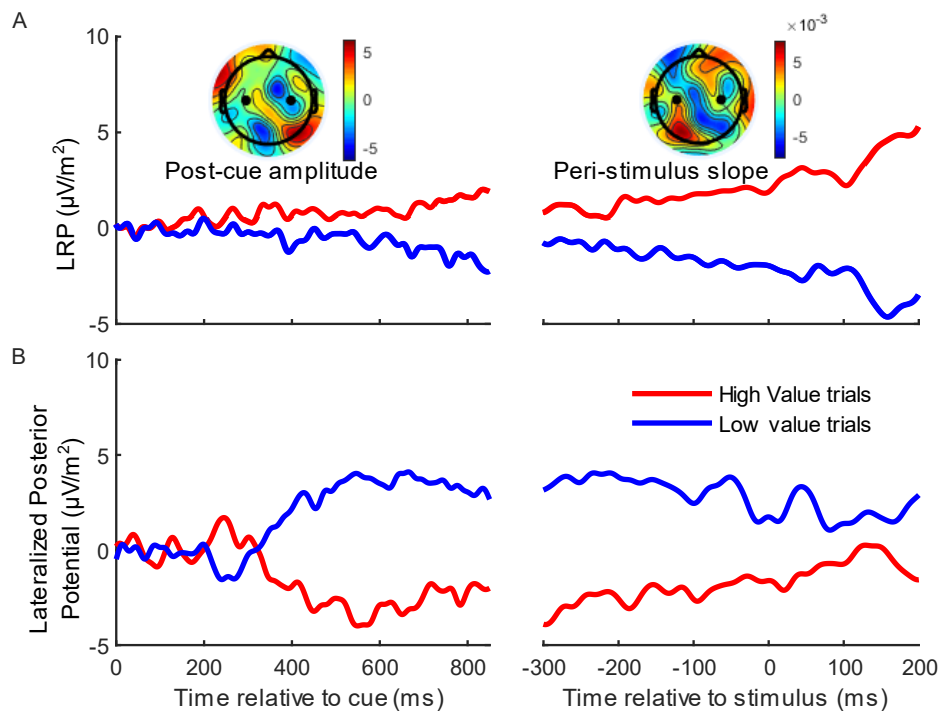


Figure 2-Figure Supplement 1. A slow-moving posterior potential interfered with measurement of the LRP between cue and motion stimulus, leading us to rely solely on Beta-band activity to examine anticipatory motor preparation. ERPs ipsilateral-contralateral to correct response, so that deflection upward corresponds to relative motor preparation in the correct direction, between cue and stimulus (left) and locked to the stimulus onset (right). A. LRP (standard sites C3/C4- see black dots in topographies), and B. Lateralized posterior potential (calculated in the exact same way as the LRP but using parietal electrodes A5 and A18 on the left; A31 and B5 on the right, Biosemi 128-channel cap). The LRP following the onset of the cue appeared to show a slowly growing bias towards the cued direction which, contrary to our findings of a tapering relative bias in Beta, persisted up to and following the stimulus onset. However, the difference topography (left inset) of left- minus right-cued trials just before stimulus onset (700-800 ms after the cue) relative to cue onset (-50-50 ms) shows that, that rather than motor preparation, the topography was dominated by a posterior potential of the opposite polarity. This slow posterior potential begins to grow at around 300 ms after the cue and then begins to decrease after around 600 ms, calling for an accounting of potential overlap effects in interpreting the LRP dynamics between cue and stimulus. The relative Beta amplitude timecourse (Figure 2B) shows that relative preparation for the high value alternative begins before 400 ms, at which time the LRP here appears quite stable. However, it is likely that the simultaneously increasing, opposing posterior potential may at that point be suppressing the expression of a motor preparation bias towards high value in the LRP. Then, as the relative Beta preparation begins to decline at around 600 ms, the posterior potential is also beginning its decline and inducing what appears as an increasing bias to high value in the LRP. The right inset topography shows the difference in slope for left and right- cued trials from -200 to +100ms relative to the stimulus. It is clear that this slow drift towards high value visible in the LRP is primarily posterior in origin. For this reason, we did not rely on the LRP to examine the anticipatory motor preparation dynamics, but rather restricted its use to the analyses of stimulus-evoked activity, and baseline corrected the signal to stimulus onset.

Table 2- Table Supplement 1. Goodness of fit metrics for main models and some with selected additional parameters.

Model	Stimulus-evoked bias	Evidence	k	G <sup>2</sup>	AIC
BurstIE	Burst	Increasing	14	39	67
SustIE	Sustained	Increasing	14	51	79
BurstSE	Burst	Stationary	13	62	88
SustSE	Sustained	Stationary	13	87	113
BurstIE + drift boost	Burst	Increasing	15	39	69
BurstIE + $s_z$	Burst	Increasing	15	38	68
SustIE + $s_z$	Sustained	Increasing	15	52	82
BurstSE + $s_z$	Burst	Stationary	14	61	89
SustSE + $s_z$	Sustained	Stationary	14	86	114
BurstSE + $sT_{ev}$	Burst	Stationary	14	58	86
SustSE + $sT_{ev}$	Sustained	Stationary	14	86	114

*In addition to the 4 main models described in our Results (recapitulated in the first 4 rows of this table), we fit several additional models to examine the effects of some differences in implementation with respect to a recent neurally-informed (NI) model of a broadly similar nature, described in Kelly et al., (2020). First, a central finding from that study, which involved an extreme speed-pressure manipulation, was that the drift-rate parameter of the NI model increased under speed pressure for the same stimulus coherence. Thus, the: “BurstIE + drift boost” model allowed an additional drift boost parameter in the high-coherence blocked condition, relative to high-coherence interleaved. This resulted in an identical G<sup>2</sup>, suggesting that in this case the much more subtle speed pressure manipulation between the conditions was not sufficient to replicate the effect. Second, the NI model of Kelly et al., (2020) had a uniformly distributed starting-level variability with a range parameter,  $s_z$ , applied independently to the constrained mean starting levels of the decision variables. This parameter did not improve our fits to any of the 4 models (listed in rows 6-9). Third, it was possible that the effect of the gradual integration of motion evidence could be captured in the SE models by allowing for variability in the evidence onset time,  $T_{ev}$ . Whereas Kelly et al., (2020) incorporated variability in accumulation onset relative to a fixed evidence onset time, it was more convenient here to incorporate a qualitatively similar feature by varying evidence onset, since accumulation onset was anchored to the onset of the LRP bolus response. We found that adding such variability, uniformly distributed with range  $sT_{ev}$ , very slightly improved performance of the BurstSE model and did not help the SustSE model. Neither were improved to an extent where they could compete with the best-fitting BurstIE model.*

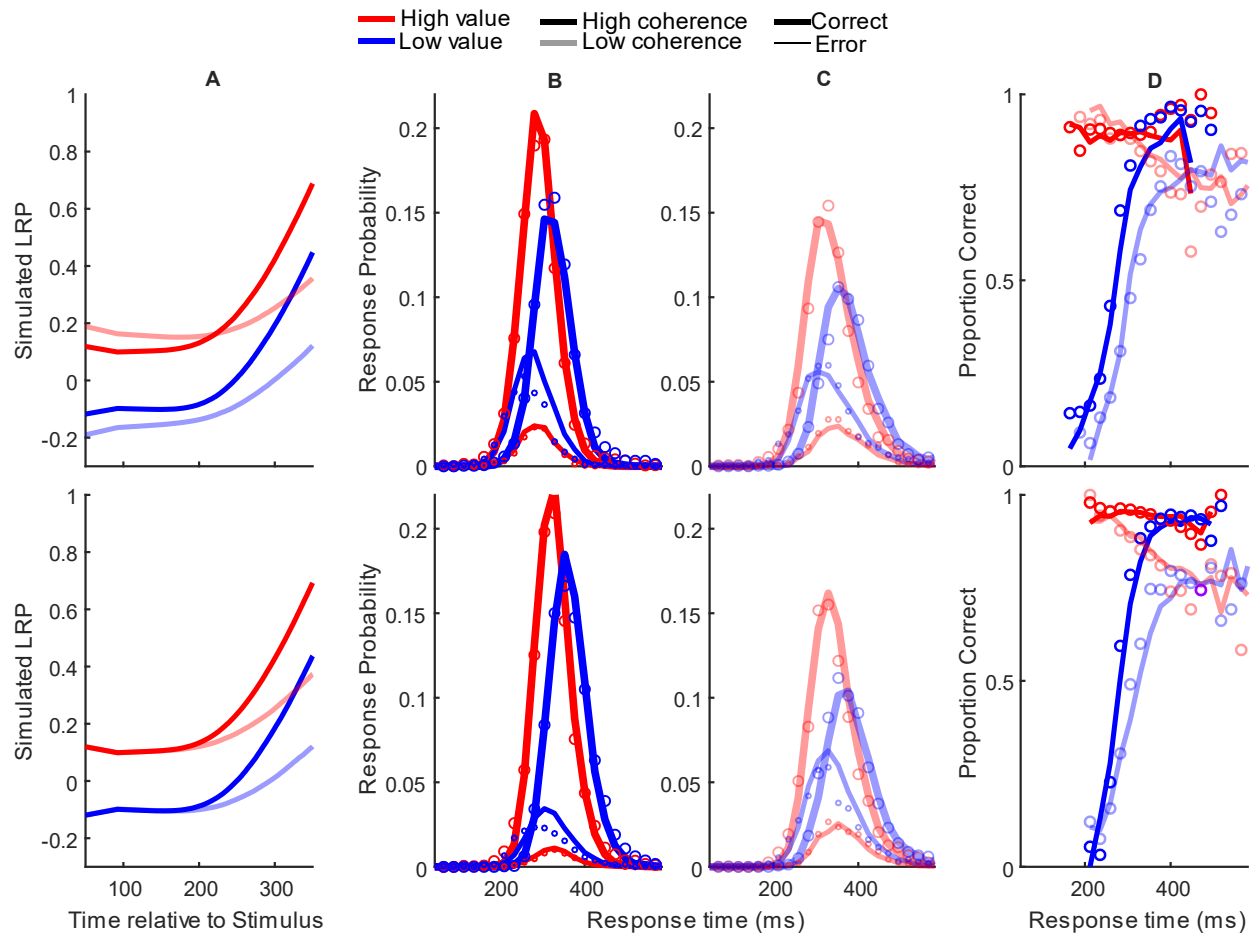


Figure 4-Figure Supplement 1. SustIE model-simulated waveforms and behavior for blocked session (top row) and interleaved session (bottom row). A Mean difference between simulated DVs; B-C Real (circles) and model-simulated (solid lines) RT distributions. D Real and model-simulated CAFs.

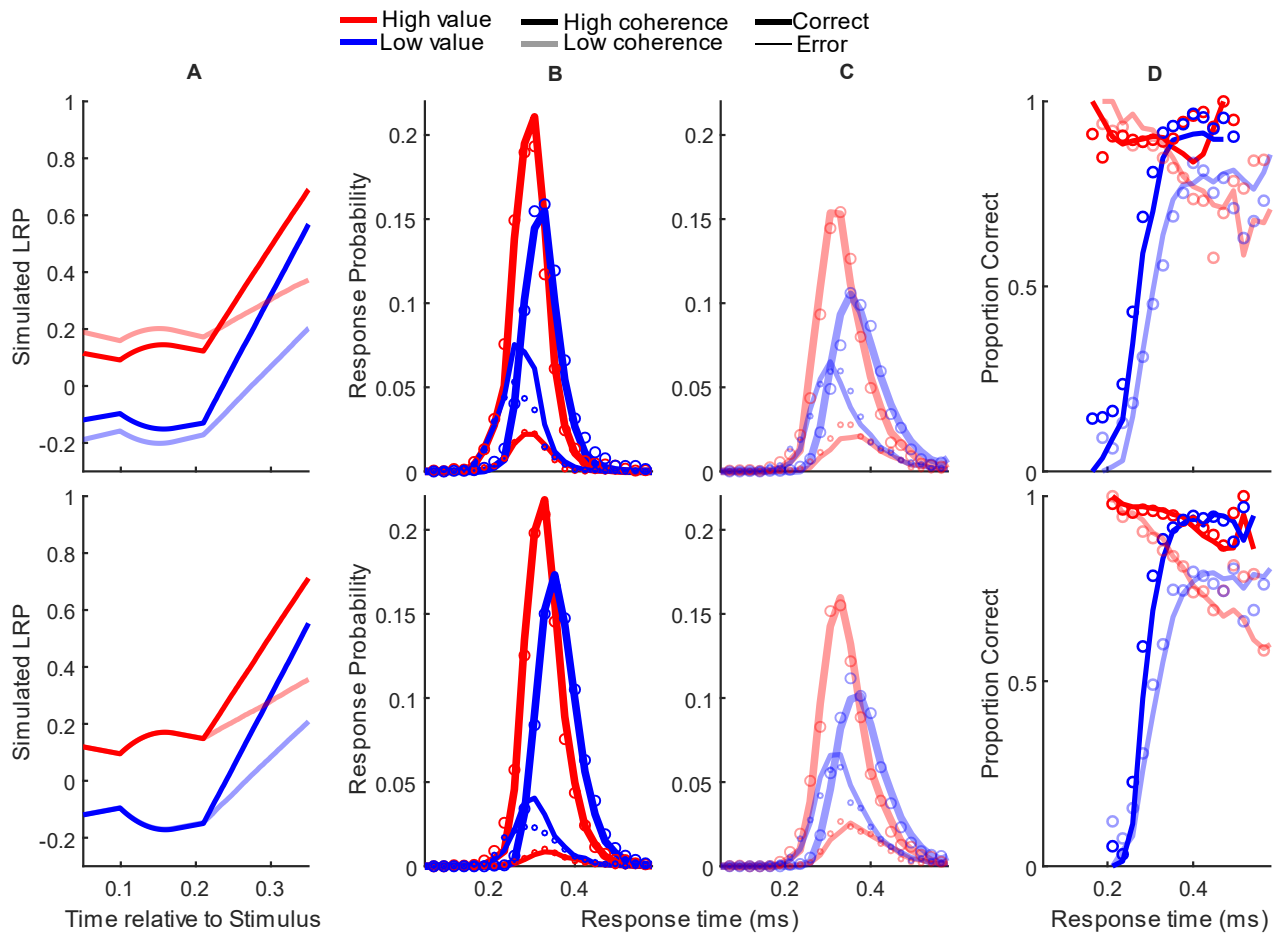


Figure 4-Figure Supplement 2. BurstSE model-simulated waveforms and behavior for blocked session (top row) and interleaved session (bottom row). A Mean difference between simulated DVs; B-C Real (circles) and model-simulated (solid lines) RT distributions. D Real and model-simulated CAFs.



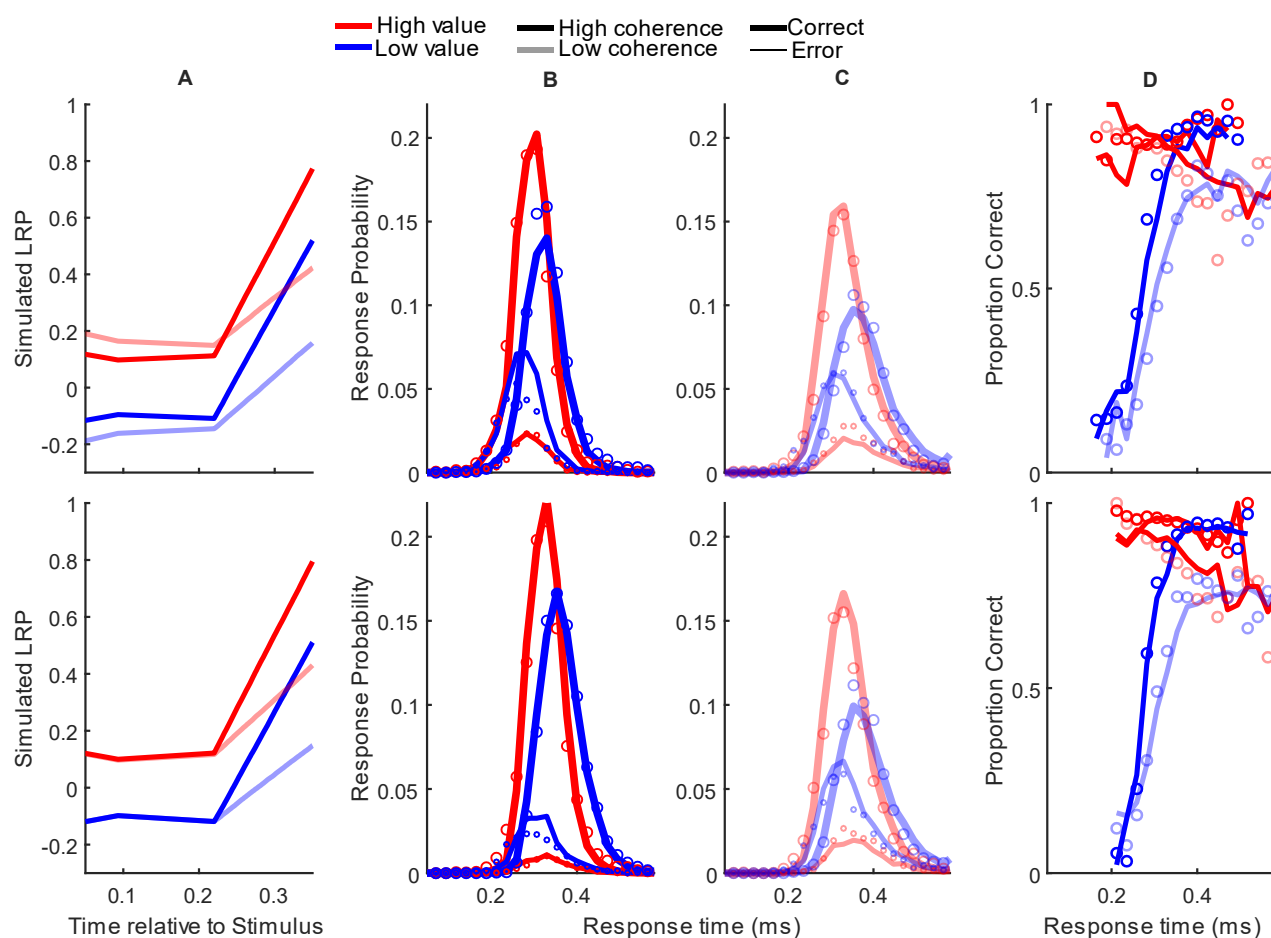


Figure 4-Figure Supplement 3. SustSE model-simulated waveforms and behavior for blocked session (top row) and interleaved session (bottom row). A Mean difference between simulated DVs; B-C Real (circles) and model-simulated (solid lines) RT distributions. D Real and model-simulated CAFs.

Figure 5-Supplementary Table 1. Beta start-points and slopes for individually-selected electrodes and C3/C4.

Parameter	Individually selected			C3/C4		
	High Coherence	Low Coherence	Interleaved	High Coherence	Low Coherence	Interleaved
$Z_c$	.32	.3	.2	.32	.36	.2
$Z_i$	.12	.002	0	.11	.06	0
$U_c$	1.36	1.09	1.3	1.25	0.96	1.17
$U_i$	1.83	1.7	1.79	1.66	1.61	1.62