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1 **Centroparietal activity mirrors the decision variable when**
2 **tracking biased and time-varying sensory evidence**

3
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26 *Decision-making is a fundamental human activity requiring explanation at the neurocognitive*
27 *level. Current theoretical frameworks assume that, during sensory-based decision-making,*
28 *the stimulus is sampled sequentially. The resulting evidence is accumulated over time as a*
29 *decision variable until a threshold is reached and a response is initiated. Several neural*
30 *signals, including the centroparietal positivity (CPP) measured from the human*
31 *electroencephalogram (EEG), appear to display the accumulation-to-bound profile*
32 *associated with the decision variable. Here, we evaluate the putative computational role of*
33 *the CPP as a model-derived accumulation-to-bound signal, focussing on point-by-point*
34 *correspondence between model predictions and data in order to go beyond simple summary*
35 *measures like average slope. In two experiments, we explored the CPP under two*
36 *manipulations (namely non-stationary evidence and probabilistic decision biases) that*
37 *complement one another by targeting the shape and amplitude of accumulation respectively.*
38 *We fit sequential sampling models to the behavioural data, and used the resulting*
39 *parameters to simulate the decision variable, before directly comparing the simulated profile*
40 *to the CPP waveform. In both experiments, model predictions deviated from our naïve*
41 *expectations, yet showed similarities with the neurodynamic data, illustrating the importance*
42 *of a formal modelling approach. The CPP appears to arise from brain processes that*
43 *implement a decision variable (as formalised in sequential-sampling models) and may*
44 *therefore inform our understanding of decision-making at both the representational and*
45 *implementational levels of analysis, but at this point it is uncertain whether a single model*
46 *can explain how the CPP varies across different kinds of task manipulation.*

47

48 *Key words: decision-making, centroparietal positivity, decision bias, non-stationary evidence,*
49 *accumulator model*

50

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52

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55

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57 the experiment; C.K. and L.S. conducted the research and analysed the data; C.K.
58 drafted the paper, which all authors critically revised and approved.

59

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61

62 **1. General Introduction**

63 Both mathematical modelling of cognitive processes and the analysis of neural and
64 behavioural data have generated important insights about human cognition.

65 Recently, the importance of combining these approaches has become increasingly
66 apparent. This triangulation of methods (sometimes referred to as model-based
67 cognitive neuroscience; Forstmann, Wagenmakers, Eichele, Brown, & Serences,
68 2011) provides several obvious advantages over traditional approaches, as neural
69 data can inform mathematical models, while models can in turn break complex
70 cognitive processes into separate mechanisms, which are easier to test using neural
71 data (Turner, Rodriguez, Norcia, McClure, & Steyvers, 2016).

72

73 A variety of approaches have now been suggested to combine cognitive
74 neuroscience and mathematical modelling (Forstmann, Ratcliff, & Wagenmakers,
75 2016; van Ravenzwaaij, Provost, & Brown, 2017). One field in which model-based
76 cognitive neuroscience has been particularly fruitful is the study of perceptual
77 decision-making (e.g. Mulder, van Maanen, & Forstmann, 2014). Perceptual
78 decisions, in which we quickly categorise sensory stimuli, directly trigger some of our
79 most basic but essential behaviour, and also provide a building block towards higher
80 cognition. Such decisions can be described by sequential sampling models, a group
81 of computational models which assume that to make a decision, we accumulate
82 sensory evidence over time until a decision threshold is reached, at which point we
83 typically initiate the corresponding motor response (Brown & Heathcote, 2008;
84 Ratcliff & McKoon, 2008; Usher & McClelland, 2001).

85

86 Importantly, although these models were developed to explain behavioural data and
87 have done so successfully in a large variety of paradigms (Huk & Shadlen, 2005;
88 Milosavljevic et al., 2010; Ratcliff, 2002; Ratcliff, Thapar, College & Mckoon, 1992),
89 they have been further validated by electrophysiological recordings in non-human
90 primates, as several studies have reported accumulation-like neuronal activity while
91 monkeys perform perceptual-decision tasks (e.g. Hanes & Schall, 1996; Shadlen &
92 Newsome, 1996; for a review see Schall, 2002; Gold & Shadlen, 2007; Hanks &
93 Summerfield, 2017). This connection between models and neural data has since
94 been successfully used to directly compare electrophysiological signals with
95 predictions made by mathematical models (e.g. Hanks, Kiani, & Shadlen, 2014;
96 Purcell et al., 2010; Purcell, Schall, Logan, & Palmeri, 2012), and provided important
97 insights into decision-making processes. For example, by analysing firing rates of
98 frontal eye field neurons, Purcell and colleagues (2010) were able to evaluate
99 different cognitive models, thereby highlighting the potential role of neural data as a
100 model selection tool.

101

102 The study of neural substrates of the decision variable (i.e. the decision-related
103 accumulation profile) in the human brain, on the other hand, has been advancing
104 more slowly. One method which is commonly used to study decision-making within
105 model-based cognitive neuroscience is functional magnetic resonance imaging
106 (fMRI). In this field, brain activity is analysed in reference to specific model
107 parameters, which has led to the association of different brain regions with specific
108 sub-processes of decision making (e.g. Forstmann et al., 2010; Heekeren, Marrett,
109 Bandettini, & Ungerleider, 2004; for a review, see Mulder et al., 2014).

110

111 In order to track the decision variable in the human brain, however,
112 electroencephalography (EEG) or magnetoencephalography (MEG, which produces
113 comparable data) are commonly used, due to their greater temporal resolution. A
114 variety of different signals have been proposed to be decision-related, ranging from
115 event-related potentials (ERPs; Philiastides, Heekeren, & Sajda, 2014; Philiastides
116 et al., 2006; Philiastides & Sajda, 2006; Pisauro, Fouragnan, Retzler, & Philiastides,
117 2017; Ratcliff et al., 2009) to changes in theta-band power (van Vugt et al., 2012),
118 and motor-related lateralised desynchronisation in beta power (Donner, Siegel,
119 Fries, & Engel, 2009; Meindertsma, Kloosterman, Nolte, Engel, & Donner, 2017;
120 Siegel, Engel, & Donner, 2011).

121

122 A particularly promising approach was introduced by O'Connell, Dockree, and Kelly
123 (2012). In a series of experiments, they identified the centroparietal positivity (CPP),
124 an ERP component which shows several key properties of the decision variable. It
125 displays a build-up over the course of the decision, reflecting the integration of
126 sensory evidence, and its crossing of a stereotyped level was shown to predict
127 reaction time (RT; Kelly & O'Connell, 2013; O'Connell et al., 2012). Importantly, the
128 CPP was shown to be independent of sensory and motor signals, as it was fully
129 dissociable from both steady-state visual evoked responses, which provide a readout
130 of sensory input, and contralateral beta power, which reflects motor activation.
131 Independence from motor signals was later confirmed in a study which directly
132 compared the CPP to motor-related beta power, and showed that while both signals
133 build up over the course of the decision, the CPP drops back to baseline levels after
134 a given threshold is reached, while beta activity persisted until a delayed response
135 (Twomey, Murphy, Kelly, & O'Connell, 2016).

136

137 Interestingly, the CPP was also observed in an auditory decision-making task,
138 highlighting its putative role as a supramodal decision signal (O’Connell et al., 2012).
139 Following their initial series of experiments, Kelly and O’Connell (2013) provided
140 further evidence supporting the role of the CPP as a decision variable by exploring
141 the CPP in a perceptual decision-making task with different levels of difficulty. This
142 manipulation is known to affect the slope at which sensory evidence is accumulated,
143 with easier stimuli leading to a steeper evidence accumulation rate. This was
144 confirmed in Kelly and O’Connell’s study based on parameter estimates derived from
145 the Diffusion model (Ratcliff & McKoon, 2008). The CPP build-up slope varied
146 according to task difficulty level, qualitatively mirroring model predictions regarding
147 accumulation rate. Hence, experimental evidence from previous studies consistently
148 indicates that summary statistics describing the CPP (such as average slope over
149 some arbitrary time window) correspond with the equivalent intuited or abstracted
150 characteristics of a decision variable.

151

152 Identifying the neural substrates of human perceptual decisions is an important goal,
153 because a compelling explanation of behaviour should marry computational
154 plausibility with biological reality (Krakauer, Ghazanfar, Gomez-Marin, Maclver, &
155 Poeppel, 2017; Marr, 2010). To move forward, we must go beyond a broad-brush
156 equivalence between brain signals and model predictions, and show that the
157 quantitative precision of sequential sampling models extends to both behaviour and
158 brain dynamics. Although the CPP appears to be a serious candidate for bridging
159 this divide, few studies have formally compared CPP profiles with the decision
160 variable exactly as predicted by sequential sampling models. Building on Kelly and

161 O'Connell's approach, Twomey et al. (2015) added a critical step to their analysis to
162 allow for a direct comparison between the model decision variable and the CPP.
163 After fitting the Diffusion model, the resulting parameters were used to simulate the
164 mean level of evidence accumulation across time predicted by the model. The
165 simulated accumulation profile and the CPP were in close agreement. This finding is
166 important, as it goes beyond comparing summary measures derived from a potential
167 neural substrate of decision-making against a set of abstract characteristics derived
168 from intuitions about model behaviour, and instead allows for a direct comparison of
169 the entire accumulation profile. Indeed, with more complex sequential sampling
170 models (e.g. those incorporating inhibition or leakage; Usher & McClelland, 2001) it
171 becomes virtually impossible to intuit how accumulation profiles may change as a
172 function of different experimental manipulations, making detailed modelling essential
173 (Purcell & Palmeri, 2017).

174

175 The current study fulfils this brief, going beyond previous work testing the role of the
176 CPP as a decision variable through formal implementation of sequential sampling
177 models. As outlined above, the CPP has only been tested in the context of a limited
178 number of manipulations (O'Connell et al., 2012; Kelly & O'Connell, 2013), and until
179 recently only the impact of decision difficulty has been compared to simulations
180 based on behaviourally constrained sequential sampling models (Twomey et al.,
181 2015). Similar analyses have since been applied to investigate the speed-accuracy
182 trade-off (Spieser et al., 2018) and under combined conditions of extreme time
183 pressure and value-based bias (Afacan-Seref, Steinemann, Blangero, & Kelly, 2018)
184 but comparisons with precise model predictions remain scarce. Hence here we
185 compared the CPP profile to exact model predictions in two separate EEG

186 experiments. These experiments tested both probabilistic decision biases, which, to
187 our knowledge, have not been previously assessed using the CPP, and non-
188 stationary evidence profiles, which we believe have not previously been examined
189 for the CPP under conditions of speeded choice. In line with previous behavioural
190 work (Mulder, Wagenmakers, Ratcliff, Boekel, & Forstmann, 2012; Spaniol, Voss,
191 Bowen, & Grady, 2011; Summerfield & Koechlin, 2010; Voss, Nagler, & Lerche,
192 2013), our estimation of model parameters revealed that decision bias affects the
193 amount of evidence required to attain response threshold, while non-stationary
194 evidence affects the detailed time-course of evidence accumulation. We then used
195 the estimated parameter values to simulate the accumulation profiles as predicted by
196 the models and compared them to the recorded CPP.

197

198 We chose two types of race accumulator models (Brown & Heathcote, 2008;
199 Heathcote & Love, 2012) to account for our behavioural data, namely, the leaky
200 competing accumulator model (LCA; Usher & McClelland, 2001), suggested to be
201 one of the most neurophysiologically plausible sequential sampling models, and a
202 simplified independent race accumulator model. Contrary to random walk models
203 such as the Diffusion model, in which evidence is integrated in a single accumulator
204 (Smith & Ratcliff, 2004), and which are motivated more by mathematical optimality
205 than neurobiological plausibility (Ratcliff et al., 2016; Usher & McClelland, 2001),
206 what we here refer to as ‘race accumulator models’ assume that evidence for each
207 response alternative is integrated in separate accumulators, which race to reach a
208 common threshold. Assuming that processes similar to these occur in the brain, with
209 each accumulator being associated with a neural population, and given the nature of
210 EEG, which records the sum of all underlying electrical activity from the scalp, we

211 propose that the CPP should be best predicted by the summed activity of both
212 accumulators in a two-choice task. Across experiments varying the two core
213 characteristics of accumulation-to-bound activity, namely the shape of accumulation
214 build-up and the extent of baseline-to-bound distance, our results show that CPP
215 dynamics can indeed closely match time-varying predictions derived under a
216 sequential-sampling modelling framework, but that this match partly reflects the
217 flexibility we enjoyed as a result of having several candidate models available.

218

219 **2. Experiment 1: Non-stationary Evidence**

220

221 Most research in the field of perceptual decision-making has focused on binary
222 choices with stationary evidence, where information remains virtually unchanged in
223 quality and intensity throughout the decision-making process (Gold & Shadlen, 2000;
224 Kelly & O'Connell, 2013; Ratcliff & McKoon, 2008; Ratcliff et al., 2010). In everyday
225 life, however, decisions typically occur in a dynamic environment, in which sensory
226 evidence is continuously changing, and several studies have drawn attention to the
227 fact that comprehensive models of decision-making have to be able to account for
228 decisions with non-stationary evidence. Researchers have hence started to use
229 decisions in response to non-stationary evidence in order to distinguish between
230 different sequential sampling models (Bronfman, Brezis, & Usher, 2016; Nunes &
231 Gurney, 2016; Tsetsos, Gao, McClelland, & Usher, 2012; Tsetsos, Usher, &
232 McClelland, 2011; Zhou, Wong-Lin, & Philip, 2009), which often offer
233 indistinguishable accounts of data from more traditional decision-making paradigms
234 (Brown & Heathcote, 2008; Ratcliff & Smith, 2004; Teodorescu & Usher, 2013;
235 Tsetsos et al., 2012).

236

237 Tsetsos et al. (2011, 2012), for example, conducted a series of experiments, using a
238 paradigm in which the evidence for a given alternative changed dynamically
239 throughout a trial to compare race accumulator (Brown & Heathcote, 2008; Usher &
240 McClelland, 2001) and random-walk models (Ratcliff & McKoon, 2008). They found
241 that the race accumulator model gave a better description of the data (Tsetsos et al.,
242 2011), and was able to account for various subtleties, including a primacy effect
243 which showed that changes in evidence had a larger impact on decisions early on in
244 the decision-making process (Tsetsos et al., 2012). Recently, Holmes, Trueblood,
245 and Heathcote (2016) showed that a simplified race accumulator model labelled
246 'piecewise LBA' could provide a good account of participants' behaviour. In that
247 study, participants were asked to discriminate between left and right motion in a
248 random dot motion task, in which, halfway through the decision-making process, the
249 motion direction switched. The best-fitting race model parameters confirmed that
250 accumulation rates were affected by the motion switch. Interestingly, while the switch
251 led to motion in the opposite direction but equal in magnitude, estimated changes of
252 accumulation rates were not symmetrical between the two accumulators, indicating a
253 difference in discrimination after the switch. Incorporating a delay between the switch
254 in evidence and the resulting change in accumulation rates was shown to improve
255 model fit, revealing that some time is necessary to take a modification of evidence
256 into account.

257

258 It is clear that dynamically changing evidence also has implications for any neural
259 signal posited to reflect the decision-related accumulation of evidence. This was
260 observed for instance in the firing rate of lateral intraparietal (LIP) neurons in non-

261 human primates. Huk and Shadlen (2005) demonstrated that additional
262 positive/negative motion pulses during a random dot motion task had persistent
263 effects on LIP activity, which increased/decreased for several hundreds of
264 milliseconds. In humans, O’Connell et al. (2012) explored the impact of changing
265 evidence on the CPP and motor-related beta band power. In a detection task in
266 which stimuli gradually decreased in contrast, the CPP (and, to a lesser extent, beta
267 power) was shown to plateau for several hundreds of milliseconds when the gradual
268 contrast decrease was interrupted by a 450 ms increase towards the baseline. In this
269 study, however, no comparisons were made between a simulated accumulation
270 profile and the recorded CPP waveform.

271

272 Here, we instead utilise a choice RT task and provide detailed modelling/simulation.
273 Participants performed a random dot motion task which required them to
274 discriminate between motion to the left or to the right. In one third of the trials, dot
275 motion remained unchanged throughout the trial (‘continuous’ condition), while in the
276 rest of the trials, it was interrupted for a 200 ms period. In these interrupted trials, dot
277 motion was replaced by either coherent motion in the opposite direction, before
278 continuing in the original direction (‘reverse’ condition), or by random motion without
279 any directional evidence (‘random’ condition; cf. Tsetsos et al., 2012). These
280 changes in motion should affect the build-up of the accumulation profile, and be
281 visible in any neural signal reflecting the decision variable. While we assumed that
282 the decision variable will ‘plateau’ during the coherent motion interruption in the
283 ‘random’ condition, predictions regarding the impact of the reversal of evidence are
284 less clear, and are likely to depend more on the specifications of the model, such as
285 the presence or absence of reciprocal inhibition. To determine exactly how a signal

286 reflecting the decision variable is affected, we simulated accumulation profiles
287 predicted by sequential sampling models. Importantly, in order to use model
288 specifications best resembling the underlying decision processes, we tested several
289 models and selected the one providing the best fit to our behavioural data. We then
290 directly compared the selected model's profiles to CPP waveforms. In so doing, we
291 confirmed the impact of time-varying evidence on the CPP profile and showed that it
292 corresponds closely to the modulations of evidence accumulation predicted by a
293 leaky competing accumulator model.

294

295 **2.1. Methods**

296 **2.1.1. Participants**

297 In line with commonly reported sample sizes in the CPP literature (e.g. Kelly &
298 O'Connell, 2013; O'Connell et al., 2012; Twomey et al., 2015), a total of 21
299 participants (eight males) were recruited. To ensure a reasonable and
300 distinguishable task performance at two different difficulty levels, each participant
301 completed a staircase procedure to establish the appropriate level of difficulty (see
302 below, 2.1.2). In line with criteria defined prior to data collection, one participant was
303 excluded from the experiment as the calibrated level of coherence exceeded 98% for
304 the 'easy' condition, leading to a sample of 20 participants (seven males) with a
305 mean age of 27.55 ($SD = 8.83$). The experiment was approved by the City,
306 University of London Psychology Department Ethics Committee.

307

308 **2.1.2. Stimuli and Procedure**

309 Participants were asked to complete a random dot motion task. The task was written
310 in Matlab (The Mathworks, Natick, U.S.A.), making use of Psychtoolbox functions
311 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). In this task, an array of white dots
312 was presented on a black screen. A proportion of dots moved coherently either to
313 the left or to the right, while the rest of the dots moved in random directions.

314 Participants were instructed to indicate the perceived motion direction by pressing a
315 button in their right/left hand for movement to the right/left. For this, digital response
316 buttons interfaced via a 16 bit A/D card (National Instruments X-series PCIe-6323,
317 sample rate 100,000 Hz) were held between the thumb and index finger of each
318 hand. Participants were seated 100 cm away from a cathode ray tube screen (size:
319 41 x 30 cm), operating at a refresh rate of 85 Hz and with a resolution of 1240 x 786.
320 A total of 300 dots, 0.04 x 0.04 degrees visual angle (dva) in size, were presented
321 within a 5 dva circular aperture. During random motion, on each frame, each dot was
322 displaced into a random direction. During coherent motion on the other hand, only a
323 subset of dots followed this random motion, while the remaining dots (defined by the
324 level of coherence, see below) moved uniformly either to the left or to the right,
325 depending on the trial. Both random and coherent dot movements occurred at a
326 speed of 3.3 dva per second. Additional to this motion, all dots were relocated to a
327 random position on the array every five frames. This process was added so that
328 participants could not determine the direction of the motion by following one specific
329 dot, instead having to consider the entire motion array.

330

331 Each trial began with a central fixation cross (size: 0.33 x 0.33 dva) for 500 ms (plus
332 a jitter of up to 1000 ms, drawn from a uniform distribution), followed by a period of

333 random motion (1000 ms plus a jitter of up to 1500 ms, drawn from a gamma
334 distribution with shape parameter 1 and scaling parameter 150¹). Since the onset of
335 moving dots on the screen is likely to produce a visual evoked potential which would
336 interfere with the recording of the CPP, this period of random motion was introduced
337 to allow for the evoked potential to occur before the onset of the decision-making
338 process. The random motion was followed by the onset of coherent motion (left/right)
339 which continued for up to 2000 ms or until the response (see Figure 1 a).

340

341 Participants completed a minimum of 100 practice trials at high levels of coherence
342 (i.e. > 80% of dots moving in one direction) to familiarise themselves with the task. In
343 order to calibrate suitable levels of difficulty for 'easy' and 'hard' trials for each
344 participant individually, a further 100 trials were completed in which the QUEST
345 (Watson & Pelli, 1983) staircase procedure, implemented in Psychtoolbox, estimated
346 the coherence level at which each participant responded correctly in 80% of trials.
347 This coherence level was then used for the 'hard' condition. The 'easy' coherence
348 level was set as 150% of the 'hard' coherence level. Participants had 1300 ms to
349 respond, and no feedback was provided during staircase trials. Overall, the
350 appropriate difficulty levels estimated for the remaining participants resulted in a
351 mean of 27.70% ($SD = 14.74$) coherence for 'hard', and 40.15% ($SD = 22.15$) for
352 'easy' trials.

353

354 After the staircase procedure, participants were asked to complete a further 100
355 practice trials which included all conditions of the main experiment, including the

¹ A gamma distributed foreperiod with a shape parameter of 1 was chosen as it is associated with a uniform hazard function (Luce, 1986).

356 different difficulties and evidence interruptions (see below). Like in the main task
357 (described next) participants now had 2000 ms to respond. During this training,
358 participants were given feedback in the form of their mean accuracy and RT every
359 10 trials. In order to introduce a moderate speed pressure, participants were
360 instructed to aim for a mean accuracy of at least 80% and a mean RT of less than
361 1000 ms throughout the task.

362

363 During the experiment, we manipulated the continuity of the evidence by introducing
364 three motion conditions, in addition to the manipulation of difficulty (see Figure 1 a).
365 One third of the trials, like the practice and staircase trials, were ‘continuous’ trials,
366 i.e. the coherent motion began after a period of random motion and remained
367 unchanged throughout the trial. In the ‘random’ condition, the coherent motion was
368 interrupted 200 ms after motion onset and replaced by a 200 ms period of random
369 motion (i.e., 0% coherence level), before being reinstated. Similarly, in the ‘reverse’
370 condition, the coherent motion was interrupted for the same time period, but
371 replaced by coherent motion in the opposite direction (see Figure 1 a). Informal
372 questioning of participants indicated that these interruptions were not perceived
373 consciously. During the main task, the interruption condition (‘continuous’, ‘random’,
374 or ‘reverse’), motion direction (left or right) and coherence level (‘easy’ or ‘hard’)
375 varied randomly from trial to trial in an equiprobable factorial design. Each participant
376 completed 16 blocks of 60 trials. After each block, participants were given feedback
377 in the form of their mean accuracy and RT. No feedback was provided for individual
378 trials.

379 **2.1.3. EEG Recording and Pre-processing**

380 During the task, we recorded participants' EEG using 64 active electrodes, placed
381 equidistantly on the scalp (EasyCap, M10 Montage) and referenced to the right
382 mastoid. Data were recorded through a BrainAmp amplifier (BrainProducts, sampling
383 rate: 1000 Hz).

384

385 The data were pre-processed in Matlab (The Mathworks, Natick, U.S.A.), using
386 custom scripts and implementing functions from the EEGLAB toolbox (Delorme &
387 Makeig, 2004). Data were re-referenced to the average reference and band-pass
388 filtered from 0.1 (low cut-off) to 45 Hz (high cut-off), using a Hamming windowed
389 finite impulse response filter. We then visually inspected the data to remove noisy
390 channels and reject large artifacts, before applying independent component analysis
391 to correct for eye blinks. Afterwards, the data were visually inspected a second time
392 in order to manually remove any remaining noise. Lastly, we used spherical spline
393 interpolation to reconstruct any channels that were previously removed. In line with
394 the procedures used in previous CPP studies (Kelly & O'Connell, 2013; O'Connell et
395 al., 2012), the data were converted to current source density (CSD) estimates to
396 increase spatial selectivity. The CSD transformation was applied using the CSD
397 toolbox, which uses a spherical spline algorithm, with the spline interpolation
398 constant m set to its default value ($m = 4$; Kayser & Tenke, 2006).

399

400 **2.1.3.1. ERP Analysis**

401 For the ERP analysis, we extracted both stimulus-locked (-200 to 2000 ms, relative
402 to coherent motion onset) and response-locked (-1000 to 100 ms, relative to the
403 button press) epochs. All epochs were baseline corrected to the average over a 200

404 ms period preceding the coherent motion onset. As only medial electrodes were
405 analysed, and initial observations revealed no difference depending on the direction
406 of motion, we collapsed over 'left' and 'right' trials. Further, since high overall
407 accuracy scores led to insufficient numbers of error trials to generate reliable ERP
408 signals, error trials were excluded.

409

410 The appropriate electrode to generate the CPP waveform was chosen individually,
411 by visually inspecting each participant's averaged ERP topography to identify the
412 centroparietal region of maximum amplitude (chosen electrodes: 1, 5, or 14, roughly
413 equivalent to electrodes Cz, CPz, and Pz in the 10-20 system; see Figure 1 d). The
414 activity in the selected electrode was averaged for each condition and for stimulus
415 and response-locked signals separately.

416

417 **2.1.4. Statistical Analysis**

418 Differences between conditions for behavioural data were inferred using ANOVAs
419 and generalized linear mixed models (GLMMs) with logistic link functions, for RTs
420 and error rates respectively. GLMMs were chosen for the analysis of accuracy data
421 since the non-normal distribution of such data will, at a theoretical level, always
422 violate the assumptions of ANOVA (Jaeger, 2008). They were implemented using
423 the Matlab fitglm command; all effects of interest (e.g. 'Difficulty', 'Interruption', and
424 their interaction) were clustered within participants and included as random effects in
425 the model specifications (e.g. Wilkinson notation: $Accuracy \sim 1 +$

426 Interruption*Difficulty + (1+Interruption*Difficulty |
427 Participant).²

428

429 In order to test the effects of the difficulty and interruption manipulations on the ERP,
430 we explored both the slopes and the amplitudes of the waveforms. First, we
431 compared the slopes between the different conditions by fitting a straight line to the
432 CPP for each participant and each condition and measuring its slope. The resulting
433 slopes were then compared in an ‘Interruption’ (‘continuous’, ‘random’, ‘reverse’) x
434 ‘Difficulty’ (‘easy’, ‘hard’) repeated-measures ANOVA.

435

436 We compared slopes during two different time intervals in the stimulus-locked data:
437 an early interval between 100 and 300 ms and a late interval between 300 and 500
438 ms relative to the onset of coherent motion. Given the interruption interval of 200 to
439 400 ms and the assumption of a small lag between stimulus presentation and
440 accumulation (typically observed in the CPP, see Kelly & O’Connell, 2013; Spieser et
441 al., 2018), we assume that the early interval reflects accumulation mainly before the
442 interruption and the late interval reflects accumulation mainly during the interruption.
443 However, since these intervals were primarily chosen based on visual inspection,
444 and Kelly and O’Connell (2013) suggested a longer 200 ms delay between the
445 evidence and its visible effect on the CPP waveform, we also repeated the analysis,
446 defining the interruption interval as a 400-600 ms time window.

447

² This represents the ‘maximal’ random effects structure (Barr, Levy, Scheepers, & Tily, 2014) which makes the model as equivalent as possible to a traditional repeated-measures ANOVA, whilst properly respecting the nature of the data.

448 Additionally, we analysed the impact of difficulty and interruption on the amplitude of
449 the waveform. Between 0 and 1000 ms in the stimulus-locked data, and
450 between -1000 to 0 ms in the response-locked data, we compared conditions using
451 an ‘Interruption’ (‘continuous’, ‘random’, ‘reverse’) x ‘Difficulty’ (‘easy’, ‘hard’) ANOVA
452 at each time point. The results were controlled for multiple comparisons using the
453 false discovery rate (FDR) approach (Benjamini & Hochberg, 1995)³.

454

455 **2.1.5. Model Fit**

456 To model the behavioural data, we used two sequential sampling models. Firstly, the
457 independent race accumulator model which is, at least conceptually, one of the
458 simplest sequential sampling models (Brown & Heathcote, 2008; Usher &
459 McClelland, 2001). In this model, evidence for each response alternative is
460 integrated in independent accumulators which race towards the decision threshold.
461 At each time point, a given accumulator i accumulates the input evidence I_i
462 supporting response alternative ‘ i ’, as well as noise N , drawn from a normal
463 distribution with mean 0 and standard deviation σ , so that the quantity accumulated
464 at each time point is described by:

$$dx_i \propto I_i + N(0, \sigma^2) \quad (1)$$

³ In this procedure, the uncorrected p -values are sorted from lowest to highest (p_i refers to the i th lowest value out of m total p -values). The largest i for which $p_i < \left(\frac{i}{m}\right) \alpha$ is identified and all p -values associated with i s smaller or equal to the identified i are considered significant.

465 The strength of input I_i depends on the mean accumulation rate v_i , which reflects the
466 quality of evidence. To remain physiologically plausible, the accumulation process is
467 restricted to positive values at each time step⁴:

$$x_i(t + 1) = \max(0, x_i(t) + dx_i) \quad (2)$$

468

469 Once either of the accumulators reaches the threshold A , the corresponding
470 response (here response 'i') is initiated. Potential variations between trials' starting
471 states are introduced by varying accumulation starting point, which is drawn for each
472 accumulator and each trial from a uniform distribution between 0 and S_z . The time
473 taken to reach the threshold, in addition to a non-decision time which represents any
474 time taken for sensory and motor processes before and after the accumulation
475 process respectively, defines the modelled RT. The non-decision time is drawn from
476 a uniform distribution with width S_{Ter} , centred on T_{er} .

477

478 In addition to the independent race accumulator model, we also used the more
479 physiologically plausible LCA model (Usher & McClelland, 2001) which introduces
480 interactions within and between accumulators. In this model, like the simpler
481 independent race model described above, evidence for each response alternative is
482 accumulated in separate accumulators which race towards response threshold A .
483 Additionally, the LCA includes a leakage parameter k as well as a parameter β for

⁴ Strictly, for physiological plausibility, the quantity accumulated should always be positive (as neurons cannot have negative firing rates) and also generally begin at a positive baseline (given spontaneous neural activity). Many of the models tested in this paper do begin at positive values, although this is not always the case for our LCA models (in line with conventional implementations of this model).

484 mutual inhibition between accumulators. Thus, in a binary decision involving the
 485 accumulators i and j , the change in activation in each accumulator is given by⁵:

$$dx_i \propto I_i - kx_i - \beta x_j + N(0, \sigma^2) \quad (3)$$

$$dx_j \propto I_j - kx_j - \beta x_i + N(0, \sigma^2)$$

486

487 Where I is the input into the accumulator and $N(0, \sigma^2)$ is noise drawn from a normal
 488 distribution with a mean of 0 and a standard deviation of σ . Again, the accumulation
 489 process is limited to positive numbers:

$$x_i(t + 1) = \max(0, x_i(t) + dx_i) \quad (4)$$

$$x_j(t + 1) = \max(0, x_j(t) + dx_j)$$

490

491 A decision is made when either of the accumulators reaches the threshold A , and the
 492 RT is made up of the time required to reach the threshold, and a non-decision time
 493 drawn from a uniform distribution centred on T_{er} with width S_{Ter} , which accounts for
 494 sensory and motor processes before and after the accumulation process.

495

496 To determine which model provided the best fit to our behavioural data, four
 497 independent race and four LCA models were tested. In all models, the response
 498 threshold A was chosen as the scaling parameter and fixed to 1. Apart from the
 499 periods of motion interruption, evidence supporting the correct response alternative
 500 was accumulated in the ‘correct’ accumulator at a mean accumulation rate $v_{correct}$,
 501 while evidence for the incorrect response was integrated in the ‘incorrect’

⁵ In our code, these equations were implemented as:

$$dx_i = (v_i - kx_{i,t-1} - \beta x_{j,t-1})dt + N(0, \sigma^2)\sqrt{dt}$$

$$dx_j = (v_j - kx_{j,t-1} - \beta x_{i,t-1})dt + N(0, \sigma^2)\sqrt{dt}$$

With $dt = 0.01s$. Hence a correction (by a factor of dt) may be required for comparison with parameters reported in some other papers based on finite difference equations.

502 accumulator at a mean rate $V_{incorrect}$. All models implemented a change in
503 accumulation rates during the interruption interval (from 200 to 400 ms relative to the
504 decision onset), but each assumed different mechanisms (Holmes et al., 2016), as
505 described below. For consistency, ‘correct’ and ‘incorrect’ accumulator labels
506 remained constant throughout each trial, such that, during the evidence interruption,
507 $V_{correct}$ and $V_{incorrect}$ still referred to the correct and incorrect responses according to
508 the initial motion direction⁶. Finally, as trial difficulty influences evidence
509 accumulation, accumulation rates were always estimated separately for easy and
510 hard trials.

511

512 Model 1 was an independent race model defined by eight parameters, assuming
513 symmetrical changes in accumulation rates during motion interruption. In
514 ‘continuous’ trials, evidence was accumulated at mean rates $V_{correct}$ and $V_{incorrect}$
515 throughout the whole trial. In ‘random’ trials, in which the evidence becomes random
516 during the interruption, we assumed that only noise was accumulated during this
517 period, i.e., $v\text{-}random_{correct} = v\text{-}random_{incorrect} = V_{incorrect}$ from 200 to 400ms after
518 decision onset. Outside of this interval, correct and incorrect rates were set to the
519 initial values $V_{correct}$ and $V_{incorrect}$. In the ‘reverse’ condition, the evidence changed
520 direction during the interruption interval, but remained at its original strength, which
521 may lead to a reversal of drift rates, i.e., $v\text{-}reverse_{correct} = V_{incorrect}$, $v\text{-}reverse_{incorrect} =$
522 $V_{correct}$. Again, outside for the interruption interval, evidence was accumulated at
523 mean rates $V_{correct}$ and $V_{incorrect}$. This describes a model with only four accumulation
524 rates ($V_{correct}$ and $V_{incorrect}$, estimated separately for easy and hard decisions), as well

⁶ In the ‘reverse’ condition, evidence during interruption supports the *incorrect* response alternative, and is integrated in the ‘incorrect’ accumulator.

525 as the parameters S_z , T_{er} , S_{Ter} , and σ^2 which were fixed between conditions (see
526 Table 1).

527

528 Instead of symmetrical changes, model 2 assumed free variation in rates with
529 changing evidence leading to a new set of accumulation rates for the ‘random’ and
530 ‘reverse’ intervals. This results in a total of 12 accumulation rates: for each difficulty
531 condition, $v\text{-continuous}_{correct}$, $v\text{-continuous}_{incorrect}$, $v\text{-random}_{correct}$, $v\text{-random}_{incorrect}$, $v\text{-}$
532 $reverse_{correct}$, $v\text{-reverse}_{incorrect}$. All other parameters (S_z , T_{er} , S_{Ter} , σ^2) were fixed
533 between conditions, resulting in a model of 16 free parameters (see Table 1).

534

535 Models 3 and 4 were identical to models 1 and 2 respectively, but also included a
536 delay parameter d to account for a potential delay between the change in evidence
537 and the change in the decision variable (Holmes et al., 2016). Note that the delay
538 introduced here is different from simple sensorial delay, caught by the encoding part
539 of non-decision time. It instead adds a time lag between the *change* in evidence and
540 accumulation rate modulation to account for potential persistence of accumulation
541 even when evidence has changed.

542

543 Finally, Models 5, 6, 7, and 8, were LCA models implementing the same modulations
544 as Models 1, 2, 3, and 4 respectively (see Table 1).

545

546 For each participant, trials with RTs faster than 180 ms or slower than 2000 ms (less
547 than 3%) were discarded. RT distributions in each condition were then summarized
548 by five quantiles for correct trials, and by the median RT value for incorrect trials (the
549 median was used due to the low number of incorrect trials in some cases). Best

550 fitting model parameters were then determined at an individual level. Modelled RTs
551 were simulated based on the equations described above and compared to RT data
552 using Quantile Maximum Probability Estimation (Heathcote et al., 2002). Parameter
553 values were adjusted using a differential evolution algorithm implemented in Matlab
554 (The Mathworks, Natick, U.S.A.; Price et al., 2005).

555

556 We compared the goodness of fit of models by calculating the mean Bayesian
557 information criterion (BIC, Schwarz, 1978) as well as the mean Akaike information
558 criterion (AIC; Akaike, 1977). These measures take into account the likelihood of the
559 model, but also penalise a model for the number of parameters used in order to
560 resolve the problem of overfitting. For our data, AIC and BIC were not in agreement
561 regarding the best overall model. We therefore made a (somewhat arbitrary)
562 decision to favour BIC, but to also present AIC in all tables for transparency. The
563 model which best fitted the data according to the BIC measure was then used to
564 generate predictions of the accumulation profile.

565

566 In addition, we also performed a recovery study to estimate the accuracy of our
567 fitting procedure. This was done by simulating 20 RT datasets using Model 5 (LCA-
568 symmetric with no delay, i.e., the lowest BIC model, see results). The simulated
569 datasets were constructed as per our empirical individual data with the 3 interruption
570 conditions and 2 difficulty levels. The number of trials also corresponded to empirical
571 data (160 trials per condition, i.e., 960 trials in total). Results of the recovery are
572 presented in Appendix A.

573 **2.1.6. Model Prediction (neurodynamics)**

574 Since EEG recordings reflect the summation of neural activity in a given area, we
575 assumed that, if the CPP is a neural correlate of the decision variable, it represents
576 the sum of all evidence accumulation. Although a binary choice may recruit separate
577 neural populations to accumulate evidence, these neural populations would likely be
578 in close proximity. An ERP component recorded at the scalp over these neural
579 populations measures the summation of electrical activity and therefore most likely
580 the sum of both accumulation processes. In order to compare the model prediction to
581 the CPP, we therefore considered the sum of the correct and incorrect accumulation
582 profiles of correct choices.

583

584 Based on the model equations described above, a total of 10,000 accumulation
585 paths (in 10 ms time steps) were computed using individual best-fitting parameters
586 obtained for each condition. To account for sensory processes, accumulation started
587 after a sensory delay (fixed to 50% of non-decision time). Evidence was then
588 accumulated until the response threshold and continued to be accumulated for a
589 short period after the threshold was reached to account for motor processes (50% of
590 non-decision time; note that we assume that accumulation continues until the offset
591 of the stimulus, i.e. during the time to reach the threshold plus the time taken to
592 make the motor response and thus stop the stimulus in our paradigm).

593

594 To match with EEG processing, the 'sum of accumulations' signal was baseline
595 corrected by subtracting the first data point value from the whole trial. Finally, we
596 averaged accumulation signals in each condition, locked to both the estimated onset
597 of the decision process (stimulus-locked) and the response (response-locked). Since

598 the stimulus-locked signal includes varying time spans of post-decision stages, and
599 we can only speculate about the behaviour of the accumulator after the response,
600 we removed simulated trials from averaging after the response (i.e. after the crossing
601 of the threshold plus 50% non-decision time). Both stimulus and response-locked
602 individual predictions were then averaged across participants, to obtain “grand
603 average” model predictions.

604

605 To compare the EEG signal with these model predictions, we recomputed individual
606 stimulus-locked CPPs, by removing trials from the average once they reached the
607 associated RT, and then recomputed the corresponding grand average. EEG signals
608 were then low-pass filtered with a cut-off of 5 Hz for better visualisation, and
609 downsampled to match the 10 ms time steps used in the model predictions. To
610 quantify the similarity between the two signals, we analysed the correlations between
611 the model predictions and the downsampled, but not low-pass filtered EEG data for
612 each difference between conditions (stimulus-locked time-window: 0 – 1000 ms,
613 response-locked time-window: -1000 – 0 ms).

614

615 **2.2. Results**

616 **2.2.1. Behavioural Results**

617 Behavioural data were collapsed over ‘left’ and ‘right’ trials. All trials with very short
618 (< 180 ms) or very long (\geq 2000 ms) RTs were excluded from the analysis (2.99%
619 of trials). The remaining data are displayed in Figure 1 c.

620

621 As expected, 'easy' decisions were faster than 'hard' decisions, $F(1, 19) = 134.96, p$
622 $< .001, \eta_p^2 = .88$. For the main effect of 'Interruption', Mauchley's test indicated that
623 the assumption of sphericity had been violated, $\chi^2(2) = 18.77, p < .001$. We therefore
624 Greenhouse-Geisser corrected the degrees of freedom ($\epsilon = .61$). There was a
625 significant main effect of 'Interruption', $F(1.21, 23.07) = 63.45, p < .001, \eta_p^2 = .77$.
626 Pairwise comparisons using Fisher's Least Significant Difference (LSD) revealed that
627 all three levels of 'Interruption' were significantly different from each other with
628 'continuous' trials leading to shorter RTs than 'random' ($p = .001$) and 'reverse' ($p <$
629 $.001$) trials, and 'random' trials showing shorter RTs than 'reverse' trials ($p = .005$).
630 There was no significant interaction, $F(2, 38) = 2.00, p = .15, \eta_p^2 = .10$.

631

632 Additionally, GLMMs showed that accuracy also differed significantly by 'Difficulty',
633 $F(1, 114) = 7.19, p = .008$, with 'easy' conditions associated with higher accuracy
634 than 'hard' conditions. 'Interruption' was also a significant predictor, $F(2, 114) =$
635 $108.88, p < .001$. The 'Interruption * Difficulty' interaction was not significant, $F(2,$
636 $114) = 2.33, p = .10$. In order to explore the differences between all three levels of
637 'Interruption' ('continuous', 'random', 'reverse'), we fitted the model a second time,
638 but setting the reference level of 'Interruption' to 'random', rather than 'continuous'.
639 We found that both the 'continuous' and the 'random' conditions were associated
640 with higher accuracy scores than the 'reverse' condition ($p < .001$). There was no
641 significant difference between the 'continuous' and the 'random' conditions ($p = .13$).

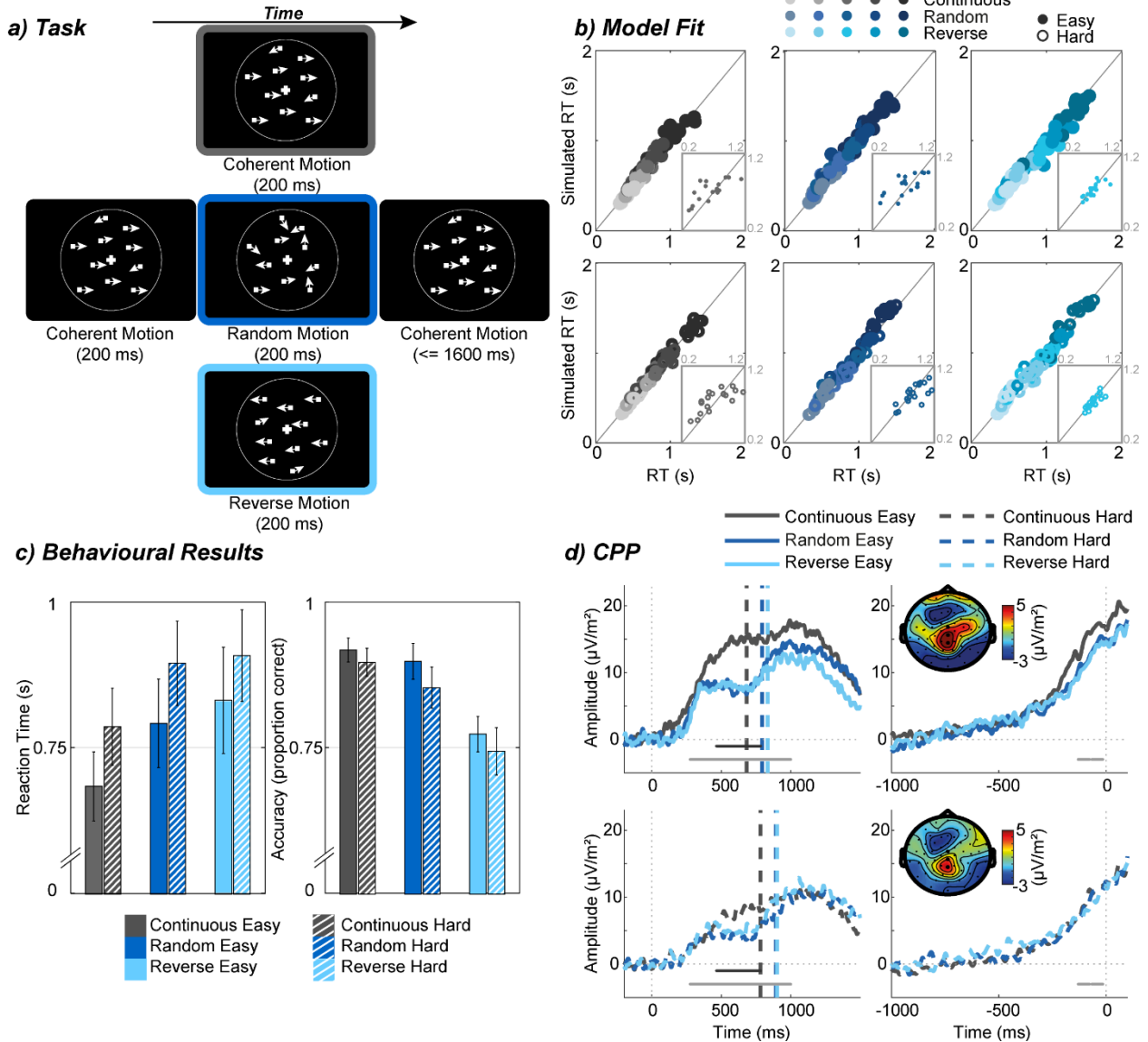
642

2.2.2. ERP Results

643 The resulting ERPs are displayed in Figure 1 d. The CPP displays a build-up over
644 the course of the decision, which seems disrupted by the interruption of evidence in

645 relevant conditions.

Figure 1



646

647 Figure 1: a) Experiment 1 random dot motion task trial procedure: in each trial, coherent motion (here: direction:
 648 right; coherence: 70%) was either continuous ('continuous' condition), or was interrupted by either random motion
 649 ('random' condition) or coherent motion in the opposite direction ('reverse' condition), before continuing in the
 650 original direction. b) Model fit: each participant's quantiles from behavioural data (x-axis) and the LCA model
 651 (Model 5) simulations (y-axis) for easy (top, filled circles) and hard (bottom, circle outlines) decisions, as well as
 652 continuous (left), random (middle) and reverse (right) conditions. Increasing quantiles (10%, 30%, 50%, 70%,
 653 90%) are represented by increasingly dark colours. Small inserted panels show observed and simulated RT
 654 medians for error trials. c) Behavioural results: mean reaction time (left) and accuracy (right) in each condition.
 655 Error bars indicate 95% confidence intervals. d) CPP results: Stimulus-locked (left) and response-locked (right)
 656 CPP waveforms for easy (top), and hard (bottom) trials. Right panels show topography averaged over the

657 stimulus-locked 0 to 1000 ms interval. Electrodes used to generate the waveform are highlighted. Vertical dashed
658 lines in the stimulus-locked CPP represent mean RTs per condition. Note that the mean RTs here are computed
659 only from trials which were included to generate the waveform and therefore differ slightly from those displayed in
660 c. Grey dots at the bottom of the waveforms indicate significance based on FDR-controlled comparisons of
661 amplitude: dark grey dots indicate a significant effect of Interruption, while light grey ones indicate a significant
662 effect of Difficulty.

663
664 First, we compared the slopes of the ERP occurring in response to evidence
665 accruing before and during the interruption period. In the first interval (100-300 ms),
666 analysis revealed that the slope of the CPP associated with ‘easy’ waveforms was
667 higher than ‘hard’ waveforms, $F(1, 19) = 12.93, p = .002, \eta_p^2 = .40$. There was no
668 main effect of ‘Interruption’, $F(2, 38) = 1.01, p = .38, \eta_p^2 = .05$, and no interaction
669 effect ($p = .82$). Conversely, in the second, interruption-driven, interval (300-500 ms),
670 the slope of the CPP was affected by the ‘Interruption’ condition, $F(2, 38) = 9.52, p <$
671 $.001, \eta_p^2 = .33$, but not by ‘Difficulty’, $F(1, 19) = .19, p = .67, \eta_p^2 = .01$, with no
672 interaction between the two factors ($p = .39$).⁷ Investigating the interruption effect
673 with Fisher’s LSD post-hoc tests showed that the slope was significantly higher in the
674 ‘continuous’ waveform than the ‘random’ and the ‘reverse’ waveforms, $t(19) > 3.40, p$

⁷ We selected two windows for slope analysis based on the timing of our stimulus (and assumptions about the time course with which information feeds through to decision areas of the brain). This approach is consistent with previous work on the CPP, but incorporates no correction for familywise error, which might raise concerns in the absence of pre-registration for the analysis. For completeness, we attempted an analysis that varied the position of the 200 ms window used to assess slope (in steps of 1 ms) and incorporated an FDR correction for these multiple comparisons. Under this approach, the slope difference associated with difficulty (100-300 ms) remains significant, but the later slope difference associated with interruption condition (300-500 ms) fails to reach significance. However, subsequent FDR-corrected analyses of amplitude provide an alternative source of evidence regarding the impact of the interruption conditions on the CPP.

675 < .003. No significant difference between the 'random' and 'reverse' conditions was
676 observed, $t(19) = .76$, $p = .46$. Since the interruption-driven time interval of 300-500
677 ms was chosen primarily based on visual inspection, we repeated the analysis using
678 a time window which assumes a 200 ms delay between the evidence and its visible
679 effect on the CPP, as suggested by Kelly and O'Connell (2013). The analysis of this
680 time window (400-600 ms) confirmed our findings (significant main effect of
681 'Interruption', $p = .005$, no other effects $p > .24$).

682

683 CPP amplitudes (as opposed to slopes) were also compared, by performing a series
684 of FDR-controlled ANOVAs. For brevity, only results showing a corrected p -value of
685 < .05 for at least 50 ms continuously are reported. In the stimulus-locked CPP, an
686 'Interruption' effect was observed between 466 and 783 ms (corrected $p < .049$; see
687 Figure 1 d, where asterisks denote statistical effects on amplitude, not the previously
688 described analysis on slopes). Fisher's LSD-corrected post hoc tests found that the
689 'continuous' waveform displayed a higher amplitude than both the 'random' (between
690 466 and 783 ms relative to the onset of coherent motion, corrected $p < .02$) and the
691 'reverse' waveforms (between 488 and 783 ms, corrected $p < .046$). There was no
692 significant difference in amplitude between 'random' and 'reverse' conditions
693 (corrected $p > .26$). Further, we found a significant effect of 'Difficulty' in the time
694 interval between 276 and 1000 ms relative to stimulus onset, with 'easy' waveforms
695 reaching higher amplitudes than 'hard' waveforms (corrected $p < .046$). There was
696 no significant interaction effect (corrected $p > .34$).

697

698 In the response-locked CPP, we found only a 'Difficulty' effect on amplitude, with
699 'easy' trials displaying a higher amplitude than 'hard' trials between -229 and 0 ms

700 relative to response. There was no main effect of 'Interruption' (corrected $p > .07$),
701 and no interaction effect (corrected $p > .9$).

702 **2.2.3. Model Fit**

703 We fitted eight sequential sampling models (four independent race and four LCA) to
704 the RT data. In each model type, models differ by assuming either symmetrical
705 (models 1,3 and 5,7) or free modulations (models 2,4 and 6,8) of accumulation rates
706 during the motion interruption period, which are applied either immediately (models
707 1,2 and 5,6) or after a free delay (models 3,4 and 7,8). For most individual
708 participants (90% by AIC; 85% by BIC) no model was strongly supported (AIC/BIC
709 improvement > 10) relative to all others. We thus averaged individual BICs (Schwarz,
710 1978) and AICs for each model to compare goodness of fit (see Table 1). It is clear
711 that the exact ordering of models was criterion dependent, although the overall
712 preference for the LCA class of model was not, with a pair of 2 (model class) x 2
713 (presence of delay) x 2 (presence of asymmetry) repeated-measures ANOVAs on
714 both AIC and BIC showing main effects of model class ($F(1, 19) = 21.81, p < .001,$
715 $\eta_p^2 = .53$ and $F(1, 19) = 13.11, p = .002, \eta_p^2 = .41$, respectively).⁸ We elected to
716 focus on BIC. The best (lowest) BIC was obtained for model 5, an LCA model with
717 symmetric variation for the interrupted accumulation rate and no delay (see Table 1).
718 Following Tukey correction, this model was reliably better than models 2, 4, 6 & 8
719 (i.e. all models allowing free modulation of accumulation rates during the interruption

⁸ For our purposes here, model comparison was a means to an end, in terms of finding a reasonable candidate for the subsequent generation of neurodynamic predictions, not an end in itself. Hence we do not present detailed results breaking down these ANOVAs, both of which included three-way interactions, but instead simply summarise all possible pairwise comparisons (see main text).

720 period; all $p < 0.001$). Without such correction, it additionally beat model 1 ($p =$
721 0.018).

722

723 Table 1: Model Comparison: BIC and AIC values for each independent race (IRA) and LCA model. The BIC and
724 AIC values of the chosen model (Model 5) are displayed in bold.

Model	Starting point interval	Decision threshold	Accumulation rates			Delay	Leak	Inhibition	Non-decision time	Non-decision time interval	Gaussian Noise SD	Number of parameters	AIC	BIC
			continuous	random	reverse									
Model 1 (IRA)	S_Z	A	V_{corr} V_{inc}	$V_{random_{corr}} = V_{inc}$ $V_{random_{inc}} = V_{inc}$	$V_{reverse_{corr}} = V_{inc}$ $V_{reverse_{inc}} = V_{corr}$	-	-	-	T_{er}	S_{Ter}	σ^2	8	3811	3850
Model 2 (IRA)	S_Z	A	$V_{continuous_{corr}}$ $V_{continuous_{inc}}$	$V_{random_{corr}}$ $V_{random_{inc}}$	$V_{reverse_{corr}}$ $V_{reverse_{inc}}$	-	-	-	T_{er}	S_{Ter}	σ^2	16	3811	3889
Model 3 (IRA)	S_Z	A	V_{corr} V_{inc}	$V_{random_{corr}} = V_{inc}$ $V_{random_{inc}} = V_{inc}$	$V_{reverse_{corr}} = V_{inc}$ $V_{reverse_{inc}} = V_{corr}$	d	-	-	T_{er}	S_{Ter}	σ^2	9	3791	3835
Model 4 (IRA)	S_Z	A	$V_{continuous_{corr}}$ $V_{continuous_{inc}}$	$V_{random_{corr}}$ $V_{random_{inc}}$	$V_{reverse_{corr}}$ $V_{reverse_{inc}}$	d	-	-	T_{er}	S_{Ter}	σ^2	17	3812	3894
Model 5 (LCA)	-	A	V_{corr} V_{inc}	$V_{random_{corr}} = V_{inc}$ $V_{random_{inc}} = V_{inc}$	$V_{reverse_{corr}} = V_{inc}$ $V_{reverse_{inc}} = V_{corr}$	-	k	β	T_{er}	S_{Ter}	σ^2	9	3789	3833
Model 6 (LCA)	-	A	$V_{continuous_{corr}}$ $V_{continuous_{inc}}$	$V_{random_{corr}}$ $V_{random_{inc}}$	$V_{reverse_{corr}}$ $V_{reverse_{inc}}$	-	k	β	T_{er}	S_{Ter}	σ^2	17	3786	3868

Model 7 (LCA)	-	A	v_{cor} v_{inc}	$v_{random_{cor}} = v_{inc}$ $v_{random_{inc}} = v_{inc}$	$v_{reverse_{cor}} = v_{inc}$ $v_{reverse_{inc}} = v_{cor}$	d	k	β	T_{er}	S_{Ter}	σ^2	10	3787	3835
Model 8 (LCA)	-	A	$v_{continuous_{cor}}$ $v_{continuous_{inc}}$	$v_{random_{cor}}$ $v_{random_{inc}}$	$v_{reverse_{cor}}$ $v_{reverse_{inc}}$	d	k	β	T_{er}	S_{Ter}	σ^2	18	3778	3865

725

726 As expected, mean accumulation rates (v) for the correct accumulator were higher in
727 easy compared to difficult conditions. In this model, interruptions and reversals in
728 evidence were modelled parsimoniously by substituting the appropriate parameters
729 during this interval, rather than fitting new ones. Note that the exact parameter
730 values returned should be treated with some caution, as a recovery study (Appendix
731 A) suggested that this LCA model has issues with identifiability, i.e., some
732 parameters can trade off to produce equally good fits (see discussion, below). Due to
733 these identifiability issues, we do not report the parameter estimates for this model
734 here, but have included them in the appendix (see Table A1).

735

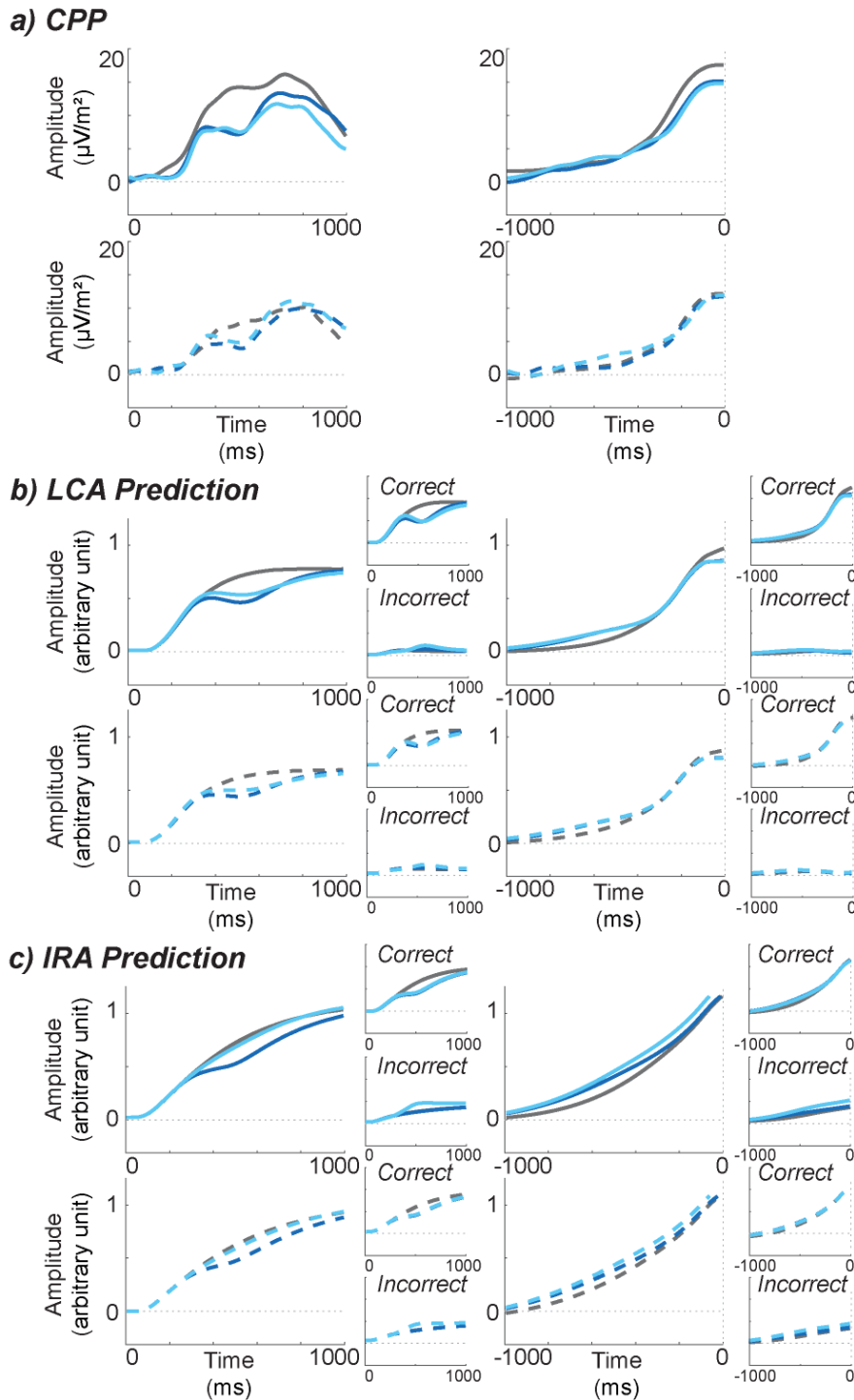
736 Figure 1 b shows the quality of the model fit by displaying each participant's
737 empirical (x-axis) and modelled (y-axis) RT quantiles (10%, 30%, 50%, 70%, 90%,
738 increasing quantiles represented by increasingly dark colours) for each interruption
739 condition as well as easy (top) and hard (bottom) trials (for behavioural fits for all
740 other models, see Appendix B). The overlap between empirical and modelled
741 quantiles indicates that the model fitted the data well.

742 **2.2.4. Model Prediction**

743 The parameters of the chosen model were then used to estimate individual
744 accumulation profiles for each condition. Figure 2 displays the mean resulting
745 predictions (b) and the corresponding EEG data (a) for stimulus (left) and response-
746 locked (right) data. The model prediction was produced by summing correct and
747 incorrect accumulators (see methods), and these contributory signals are shown
748 separately as insets. Visual inspection shows that the EEG and predicted profiles are
749 qualitatively very similar. With stimulus-locking, both profiles show an initial build-up
750 which is slower (lower slope) in ‘hard’ (dashed lines) compared to ‘easy’ (solid lines)
751 conditions, but similar across interruption conditions. Both profiles also show that the
752 ‘continuous’ waveforms continue the build-up, while ‘random’ and ‘reverse’
753 waveforms display a plateau at approximately the same time, before continuing to
754 build up. A further similarity between the model prediction and the EEG signal is the
755 unexpected finding of a near complete overlap of the ‘random’ and ‘reverse’
756 conditions during the interruption period.

Figure 2

—	continuous easy	- - -	continuous hard
—	random easy	- - -	random hard
—	reverse easy	- - -	reverse hard



757

758

759

760

761

762

Figure 2: Decision variable (empirical and simulated): a) CPP waveform for easy (top, solid) and hard (bottom, dashed) trials, as well as stimulus (left) and response-locked (right) data. The CPP here has been filtered and downsampled to match model predictions. b) Accumulation profile (correct and incorrect accumulator summed) per Interruption condition as predicted by the best-fitting LCA model, for easy (top, solid lines) and hard (bottom, dashed lines) trials, as well as stimulus (left) and response-locked (right) data. Correct and incorrect

763 accumulators were summed to form the prediction, so these contributory signals are shown separately as smaller
764 insets.c) Accumulation profile as predicted by the best-fitting independent race accumulator (IRA) model. Details
765 as in part b.

766 While a degree of positive correlation over time between EEG signals and model
767 predictions is to be expected for any ERP that grows across the RT period, the ability
768 to predict differences between experimental conditions is more challenging and
769 therefore more convincing. Hence, to quantify similarities between model predictions
770 and neurodynamic data, we analysed the correlation between *differences* of
771 conditions (differences between ‘continuous – random’, ‘continuous – reverse’, and
772 ‘random – reverse’, for both easy and hard, as well as stimulus-locked and
773 response-locked signals, resulting in a total of 12 correlations between the model
774 predictions and the downsampled EEG; see ‘Model Prediction (neurodynamics)’).
775 We found that 9 out of 12 tests revealed significantly positive correlations ($r_{mean}(98) =$
776 $.67$ $p_{mean} < .001$). All significant positive correlations remained significant after
777 Bonferroni correction. Since ‘random’ and ‘reverse’ profiles largely follow the same
778 trajectory, correlations between EEG and model signals reflecting the difference
779 between these two conditions were naturally the lowest, and in fact, non-significant
780 in some cases. The most meaningful correlations are therefore those between
781 signals reflecting the difference between ‘continuous’ and ‘random’, and ‘continuous’
782 and ‘reverse’ conditions, specifically the stimulus-locked signals, as the manipulation
783 in this experiment targeted the stimulus-locked trajectory of the accumulation. These
784 correlations remained significant after Bonferroni correction ($r_{mean}(98) = .79$, $p_{mean} <$
785 $.001$).

786

787 For reasons of concision, with eight models, our main focus when assessing the
788 overlap between model predictions and EEG was on the model which best predicted

789 the behavioural data. However, we also assessed the extent to which the winning
790 model from the other broad category (independent race model 3) could predict
791 accumulation signals resembling the CPP. Indeed, behaviourally, this model was
792 almost indistinguishable from LCA model 5 in terms of its ability to capture RTs.
793 Neurodynamic predictions for independent race model 3 are shown in Figure 2 (c).
794 As can be seen, although the global accumulation pattern is present, the
795 independent race model does not predict the empirical observation of no difference
796 during the interruption period between the ‘random’ and ‘reverse’ conditions.
797 However, although for this model the raw predictions looked rather less well matched
798 to their corresponding EEG signals, correlations based on differences between
799 conditions followed a broadly similar pattern to that observed for LCA model 5, i.e.,
800 the best fitting independent race model also did a good job of predicting the time-
801 varying ordering of EEG signals in different conditions (10 out of 12 tests revealed
802 significant correlations after Bonferroni correction $r(98) = .51, p = .001$). This
803 highlights that the correlations used here should not be used in isolation in order to
804 evaluate different models.

805

806 **2.3. Discussion Experiment 1**

807 In the first experiment, we tested the impact of non-stationary evidence on the CPP,
808 a potential neural substrate of the decision variable. Assuming that a change in
809 evidence must necessarily induce a change in the accumulation profile, the CPP
810 waveform should display a similar time-varying build-up in order to support its role as
811 a decision variable signal. To test this, we observed the CPP under three different
812 conditions: a ‘continuous’ condition in which the evidence was constant throughout
813 the trial, a ‘random’ condition in which the evidence was stopped for a brief interval

814 and replaced by random noise, and a 'reverse' condition in which the evidence was
815 reversed to support the opposite response alternative for a brief period. We also
816 added a more established manipulation (task difficulty) as a positive control. We
817 expected that the continuous condition would lead to the stereotypical, smooth build-
818 up, while the random and reverse profiles should deviate from this build-up to
819 varying extents. Critically, however, we went beyond intuitive predictions about the
820 interrupted decision variable, by first using our RT data to identify and fine-tune a
821 plausible behavioural model, and then using this model to formulate exact
822 predictions for the CPP under the assumption that this spatially diffuse EEG
823 component should represent a sum of accumulators within a race-model framework.
824 As we expand below, the resulting correspondence between model predictions and
825 CPP was striking.

826

827 Both evidence interruption and difficulty manipulations had the expected effects on
828 participants' performance, with faster and more accurate responses in 'easy' than
829 'hard' trials, and when evidence was 'continuous'. The slowest and least accurate
830 responses were observed in 'reverse' trials, while the 'random' condition lengthened
831 RT compared to continuous trials, with a less clear impact on accuracy. Hence,
832 interrupted trials led to worse performance, with evidence reversal disrupting the
833 decision more than a simple pause. These findings are broadly in line with previous
834 research (Holmes et al., 2016; Huk & Shadlen, 2005; O'Connell et al., 2012; Tsetsos
835 et al., 2012).

836

837 We infer that these changes in performance were caused by modulations of
838 decision-related evidence accumulation. It is well-established that difficulty affects

839 the slope of accumulation, with easier stimuli leading to steeper evidence
840 accumulation (Brown & Heathcote, 2008; Kelly & O'Connell, 2013; Ratcliff &
841 McKoon, 2008; Ratcliff & Rouder, 1998). The interruption of evidence, on the other
842 hand, should lead to an interruption in accumulation. To formalise this account of the
843 behaviour we observed, we tested several LCA and independent race accumulator
844 models, and found that an LCA model with symmetrical changes of accumulation
845 rates during the epoch of interruption (and for different difficulty levels) provided the
846 best account of our RT data (although other models were viable).

847

848 We hypothesised that a pause in evidence would cause the accumulation to stop
849 and plateau for the duration of the interruption interval. The impact of the 'reverse'
850 condition on the accumulation profile is somewhat harder to predict intuitively, and is
851 probably more dependent on the specifications of the model. For instance, the
852 assumption of reciprocal inhibition between accumulators may attenuate the impact
853 of evidence reversal. Specifically, the accumulator corresponding to the initial
854 direction of dot motion may inhibit the accumulator receiving the reversed evidence
855 in most trials, hence limiting accumulation growth during the reversal period. Issues
856 like these led us to emphasise modelling in formulating predictions.

857

858 We used the estimated parameters from our best-supported LCA model to simulate
859 the accumulation profiles (and, in particular, their sum) associated with each
860 condition, and directly compared the resulting patterns to the CPP. We found
861 considerable overlap between the model predictions and the neural signal, even
862 though these profiles were not fitted to one another directly. As previously reported
863 (Kelly & O'Connell, 2013; Twomey et al., 2015), task difficulty affected the slope of

864 the CPP, with lower build-up rates in 'hard' decisions. A very similar difference
865 appeared in model predictions. Furthermore, we obtained novel evidence that both
866 model predictions and the CPP showed the same gradual build-up in the
867 'continuous' condition, and interruption of this build-up (which plateaued before
868 continuing to build up approximately 300 ms later) in the 'random' and 'reverse'
869 conditions. Interestingly, model predictions also mimicked the CPP signal in terms of
870 the unexpected similarity between the 'random' and 'reverse' waveforms. These
871 patterns are particularly telling as they show an overlap between neural data and
872 evidence accumulation which might not have been predicted based on intuitive
873 reasoning alone. Our results build on previous research which found that the
874 evolution of the CPP is sensitive to a brief interruption of evidence (O'Connell et al.,
875 2012) by testing additional conditions, in a choice rather than simple RT task, and
876 making more precise model-derived predictions. Overall, the similarities we observed
877 seem to support the role of the CPP as a neural substrate of decision-making.

878

879 An additional finding worth noting is the delay in the disruption of the CPP build-up
880 compared to the timing of the evidence interruption. While the interruption of motion
881 took place between 200 and 400 ms after stimulus onset, the divergence in CPP
882 amplitude between 'continuous' profiles and the two interrupted profiles was
883 observed around 470-780 ms post stimulus. This finding supports the role of the
884 CPP as an accumulation signal, rather than a mere sensory signal, which would
885 arguably display a faster reaction in response to the change in evidence, suggesting
886 that it represents a higher-level integration of evidence.

887

888 The details of our best-fitting model are somewhat suggestive regarding the way
889 evidence accumulation follows from operations occurring in sensory regions of the
890 brain. Holmes et al. (2016) found that a change in evidence was better explained by
891 a new, independent accumulation rate, rather than a symmetric change of rates,
892 even when the change in evidence itself was symmetric. We instead found that a
893 change in evidence could be explained by a (more parsimonious) swap in
894 accumulation rate during the interruption interval. Essentially, Holmes et al. (2016)
895 found steeper accumulation rates after evidence reversal, while our results support a
896 symmetrical rate change during the reversal period. In fact, some non-linearity in the
897 sensory representation of a time-varying motion signal is to be expected (with the
898 waterfall effect offering a well-known example of repulsive sensory after-effects,
899 which are themselves complemented by assimilative tendencies; Addams, 1834;
900 Yarrow, Minaei, & Arnold, 2015). However, the exact time-course of such effects are
901 somewhat challenging to predict. The difference in findings here relative to Holmes
902 et al. (2016) may perhaps be explained by the different task procedures, as we used
903 brief perturbations while the evidence in their study remained reversed for the rest of
904 the trial. It is conceivable that sensory evidence rebounds after a change, perhaps
905 via sensory repulsion, and is thus accumulated faster, but only after some delay,
906 which is why Holmes et al. observed it and we did not. It is interesting to note that
907 even for our independent race models (which were more equivalent to Holmes et
908 al.'s piecewise LBA) a symmetric change of rates proved sufficient in our
909 experiment. Differences between our findings and those reported by Holmes et al.
910 (2016) may further be due to methodological differences in the way the models were
911 fitted to the data. While in the current study, we used Quantile Maximum Probability
912 Estimation, Holmes et al. (2016) fitted reaction time distributions using hierarchical

913 Bayesian methods, which may be sensitive to different subtleties in the data, leading
914 to different findings.

915

916 Another divergence between the two studies is that while Holmes et al.'s best model
917 introduced a delay between the presentation and the incorporation of the new
918 evidence, explaining the temporal lag between the change in evidence and its
919 behavioural consequences, positive evidence for this delay was not observed in the
920 current study. This difference may be explained by the type of model used. The LCA
921 model implements reciprocal inhibition between accumulators, which presumably
922 smooths accumulation-rate variations and produces a slow response to the change
923 in evidence without the need for a delay parameter. In the case of independent
924 accumulators on the other hand, as in Holmes et al.'s piecewise LBA, a delay
925 parameter is necessary to model the slow response to changing evidence (note that
926 our results using independent race accumulator models were consistent with Holmes
927 et al.'s findings). We hence confirm that a change in evidence is explained by
928 change in accumulation rates, and that some time is necessary for those changes to
929 feed through and become visible in the decision variable. However, while a delay
930 parameter was previously introduced to account for this temporal lag, we propose
931 that it could naturally arise from reciprocal inhibition between accumulators, as
932 implemented in the LCA model. Note, however, that our conclusion favouring an
933 LCA model without any delay was dependent on our decision to elevate BIC over
934 AIC in model comparison, and that a model with delay performed similarly well.

935

936 Finally, although LCA complexity seems advantageous in this case, it is also known
937 to induce parameter recovery issues and has been described as a model in which

938 different combinations of parameters values result in similar reaction time
939 distributions (Miletić et al., 2017). In a recovery study (Appendix A) we also observed
940 poor recovery for several of the parameters, with the implied trade-off being
941 consistent with that observed by Miletić et al.'s (2017). Presumably, the values of
942 common fractions of accumulation rates, leakage and inhibition trade off, making
943 accurate estimation of parameter values hard to achieve. Importantly, however, we
944 additionally observed that this only had a moderate impact on CPP predictions
945 derived from the fitted parameters, most probably because parameters also trade off
946 in the accumulation signal. Hence, although difficulties of parameter estimation must
947 be considered when one draws conclusions on parameter values, investigation of
948 derived accumulation signals may be less affected.

949

950 **3. Experiment 2: Decision Bias**

951

952 Experiment 1 suggested that the CPP reflects the complex decision variable
953 generated by a requirement to track time-varying sensory evidence. However, a
954 viable neurodynamic correlate should respond appropriately to a wide range of
955 manipulations known to affect the decision process. In Experiment 2, we went on to
956 test the effects of decision biases on the CPP. Probabilistic decision biases are
957 associated with strong behavioural effects, and can often be explained using
958 sequential sampling models by varying just one parameter (Summerfield & de
959 Lange, 2014; but see Rae, Heathcote, Donkin, Averell & Brown, 2014). In a
960 sequential sampling process, evidence is accumulated from a given starting point
961 towards a threshold. With the introduction of a bias towards a given alternative (e.g.
962 a greater a priori likelihood that that alternative will be evidenced) the starting point

963 moves towards the respective threshold, thereby decreasing the amount of evidence
964 required to make the choice in favour of the biased alternative (Bode et al., 2012;
965 Gao, Tortell, & McClelland, 2011; Mulder et al., 2012; Spaniol et al., 2011;
966 Summerfield & Koechlin, 2010; Teodorescu & Usher, 2013; Voss et al., 2013). In
967 contrast to Experiment 1, in which the shape of the accumulation process was
968 affected, here, we set out to investigate the impact of varying the magnitude of
969 accumulated evidence required for a decision on the CPP waveform. To our
970 knowledge, the impact of probabilistic decision biases on the CPP has not been
971 tested so far.

972

973 The neurodynamics of biased decisions have nonetheless been explored before in
974 other ways. Rorie, Gao, McClelland, and Newsome (2010) presented monkeys with
975 a binary motion-discrimination task in which the reward for the two choices was
976 either equal or unequal. Rewards primarily influenced LIP firing rates prior to the
977 motion onset, with unbalanced payoffs leading to a baseline shift towards the
978 rewarded threshold. These findings support the notion of a starting point difference in
979 accumulation for biased decisions. No difference in the slope of the build-up in firing
980 rate throughout the decision was observed. The same finding of a shift in baseline
981 activity and unaltered slopes in LIP firing rates was supported when instead of
982 unequal payoffs, predictive directional cues were used in a motion discrimination
983 task (Rao, DeAngelis, & Snyder, 2012). Similarly, it has been shown that firing rates
984 in neurons which show a build-up to threshold profile associated with a given choice
985 show a reduction in baseline activity with decreasing probability of this choice (Basso
986 & Wurtz, 1998; Dorris & Munoz, 1998), further supporting the role of starting point
987 activity in decision biases.

988

989 Evidence regarding biased neural correlates of evidence accumulation in humans
990 remains somewhat scarce. EEG research has focused primarily on motor signals to
991 track decision biases. Noorbaloochi et al. (2015) recorded human EEG during a
992 decision task with either biased or unbiased payoffs and explored the lateralised
993 readiness potential (LRP) as a signal reflecting evidence accumulation. In line with
994 findings from non-human primates, it was found that in biased decisions, the LRP
995 amplitude was shifted towards the alternative associated with the higher payoff prior
996 to stimulus onset, suggesting a starting-point difference. Additionally, de Lange et al.
997 (2013) concluded that it is a variation in accumulation starting point which accounts
998 for bias-related activity. Using MEG, de Lange and colleagues found that motor-
999 related activity in the beta frequency range displayed a pre-stimulus bias in the
1000 direction associated with the biased alternative. Together, these data suggest that
1001 biases push accumulation signals prior to the accumulation onset towards the
1002 threshold, without affecting the accumulation slope. However, recently Afacan-Seref
1003 et al. (2018) have reported somewhat different results in a study recording the CPP
1004 and LRP during binary choice with strongly biased rewards and extreme time
1005 pressure. They modelled an accelerating accumulator and found effects on the slope
1006 of accumulation, with some specific predictions regarding slow, low-valued choices
1007 mirrored in the CPP. We return to this study in the discussion.

1008

1009 To our knowledge, the effects of probabilistic decision biases on CPP profiles have
1010 not yet been explored. We therefore set out to explore the CPP waveform under
1011 different bias conditions. We presented cues which either provided information
1012 regarding the likely direction of subsequent motion or gave no directional

1013 information. Based on the literature summarised above, we expected that the
1014 presence of a directional cue would lead to a shift in accumulation starting point,
1015 decreasing the baseline-to-threshold distance in the accumulator corresponding to
1016 the cued response. Regarding the CPP waveform, this baseline variation would
1017 appear as a modulation in amplitude, since the CPP computation requires a baseline
1018 correction (i.e. the decreased baseline-to-threshold distance in correctly cued trials
1019 would translate to a decrease in the magnitude of the accumulation). However, if we
1020 assume that the CPP reflects the sum of both accumulators, the CPP waveform
1021 should also be affected by changes occurring in the accumulator opposed to the cue.
1022 If a decreased starting point in the non-cued accumulator co-occurs symmetrically
1023 with the increased starting point in the cued accumulator, it is possible that we would
1024 observe no difference in the waveforms. Again, fitting a sequential sampling model to
1025 the resulting behavioural data and directly comparing accumulation profiles
1026 simulations to the recorded CPP waveforms is crucial to yield insights into the role of
1027 the CPP as an accumulation signal.

1028 **3.1. Methods**

1029 Methods were, unless otherwise stated, identical to Experiment 1.

1030 **3.1.1. Participants**

1031 Twenty participants (five males), with a mean age of 30.15 ($SD = 7.28$) were
1032 recruited. All participants met the pre-defined requirement to achieve an average
1033 accuracy score of 80% in the random dot motion task at a coherence level no
1034 greater than 90% (i.e. 90% of dots moving coherently). Each participant took part in
1035 a session lasting between 2 and 2.5 hours.

1036 3.1.2. Stimuli and Procedure

1037 All participants first completed a minimum of 50 practice trials at a coherence level of
1038 80%. During the practice trials, feedback was provided after each trial
1039 ('correct'/'incorrect'). Afterwards, each participant completed 100 trials without
1040 feedback in order to establish an appropriate level of difficulty for the experiment via
1041 a QUEST staircase procedure targeting 80% correct. The resulting average level of
1042 coherence was 32.25% ($SD = 27.92$).

1043

1044 For the main experiment, each participant completed 450 trials. The trial procedure
1045 is displayed in Figure 3 a. In each trial, a fixation cross was followed by a cue (500
1046 ms) that consisted of two arrows, one pointing to the left, and one pointing to the
1047 right. In one third of the trials, both arrows were white, indicating no specific direction
1048 ('uncued' trials), while in two thirds of the trials, one arrow was yellow, providing a
1049 cue towards a given direction. Left-pointing and right-pointing cues were
1050 equiprobable. In each trial, the cue was followed by random dot motion, i.e. at a
1051 coherence level of 0%. After the random motion, the coherent motion started
1052 (left/right) and lasted up to 1300 ms or until the response. Note that the deadline is
1053 shorter here than in experiment 1, due to the decreased difficulty of the task. If a
1054 directionally specific cue was given, the subsequent dot motion corresponded with
1055 the cue direction 80% of the time ('congruent' trials), and opposed it in 20% of trials
1056 ('incongruent' trials). No feedback was provided after each trial, but every 60 trials,
1057 participants took self-timed breaks during which they were provided with feedback in
1058 the form of mean accuracy scores and RTs over that period.

1059

1060 **3.1.3. Statistical Analysis**

1061 In order to analyse the impact of the different cue conditions on the ERP waveform,
1062 we again compared both the slope and the amplitude between conditions. Like in
1063 Experiment 1, we compared the build-up rate by fitting a straight line to the
1064 waveform. The chosen time intervals to which we fitted a line were 200 to 350 ms for
1065 the stimulus-locked CPP, and -200 to -150 ms for the response-locked CPP (Kelly &
1066 O'Connell, 2013). The resulting slopes were then compared using a one-way
1067 ANOVA to compare 'congruent', 'incongruent', and 'uncued' waveforms.

1068 **3.1.4. Model Fit**

1069 Again, independent race accumulator and LCA classes of models were used to
1070 model RT data. Within each class we tested a total of five different models, all
1071 accounting for bias conditions using starting point modulations, but assuming
1072 different mechanisms in order to account for different bias conditions.

1073

1074 Model 1 was an independent race model assuming that cues induced changes of
1075 accumulation starting point in the accumulator corresponding to the cued response.
1076 In 'cued' trials, the lower limit of the starting point distribution, Z , was increased by
1077 the bias parameter in the cued accumulator, and was set to 0 in the accumulator
1078 opposite to the cue. In 'uncued' trials, the value of Z was fixed to 0 in both
1079 accumulators. Trial-to-trial starting point variability was introduced, such that each
1080 accumulator starting point was drawn from a uniform distribution on the interval [Z
1081 $Z+S_z$]. Hence, on average, the starting point was higher in the cued accumulator
1082 than the accumulator opposite to the cue, and both accumulators in the neutral
1083 condition. Note that this results in starting point changes in the 'correct' accumulator
1084 in congruent trials and the 'incorrect' accumulator in 'incongruent' trials. Specifically,

1085 the bias parameter should favour the 'correct' accumulator in 'congruent' trials and
1086 the 'incorrect' accumulator in 'incongruent' trials. All other parameters were fixed
1087 between conditions, resulting in a model with a total of seven parameters (see Table
1088 2).

1089

1090 Models 2 and 3 were also independent race models implementing starting point
1091 variations, but now impacting both cued and opposite accumulators. Model 2
1092 assumed symmetrical changes while model 3 assumed free variations. In model 2,
1093 again, the lower limit of the starting point distribution Z was fixed to 0 in the
1094 accumulator opposite to the cue, and was increased by the bias parameter in the
1095 cued accumulator. In this case however, in 'uncued' trials, the value of Z was fixed in
1096 both accumulators to half of the bias parameter value. Again, each accumulator
1097 starting point was drawn from the interval $[Z, Z+S_2]$. Therefore, on average, starting
1098 point variations of equal magnitude but opposed sign were applied in the cued and
1099 the opposite accumulators compared to the neutral condition, leading to opposite
1100 effects on the 'correct' and 'incorrect' starting point in 'congruent' and 'incongruent'
1101 trials. Model 3 assumed similar mechanisms, with free rather than symmetrical
1102 changes in 'cued' compare to 'uncued' trials. Here again, Z was fixed to 0 in the
1103 accumulator opposite to the cue, and increased by the bias parameter in the cued
1104 accumulator. In this case however, Z was also free to vary in 'uncued' trials. As such,
1105 free variations of the lower limit of starting point interval occurred in 'cued' compared
1106 to 'uncued' trials. Again, note that this translated into inverse effects on 'correct' and
1107 'incorrect' accumulators between 'congruent' and 'incongruent' trials (see Table 2)
1108 but without assuming that uncued accumulators started (on average) midway
1109 between congruent and incongruent ones. All other parameters were fixed between

1110 conditions, resulting in a total of seven parameters in model 2 and eight parameters
1111 in model 3 (see Table 2).

1112

1113 Finally, models 4 and 5 tested whether cues also influenced the rate of evidence
1114 accumulation, again assuming either symmetrical or free variations. Model 4
1115 implemented symmetrical starting point variation as in model 2, plus symmetrical
1116 changes in accumulation rates. V_{cued} was added to the cued accumulator rate, and
1117 was subtracted from the opposite accumulator rate. In model 5, assuming free
1118 changes, starting point variations were implemented as in model 3, and V_{cued} was
1119 added to the cued accumulator rate while V_{opp} was subtracted from the opposite rate.
1120 Again, note that the 'cued' accumulator was 'correct' in 'congruent' trials and
1121 'incorrect' in 'incongruent' trials. These manipulations resulted in a total of eight and
1122 ten parameters in models 4 and 5, respectively (see Table 2).

1123

1124 Model 6 to 10 were LCA implementations of Model 1 to 5 respectively (see Table 2).
1125 Like in Experiment 1, best-fitting model parameters were determined at the individual
1126 level. Trials with RTs faster than 180 ms or slower than 1300 ms (less than 6%) were
1127 discarded.

1128 **3.2. Results**

1129 **3.2.1. Behavioural Results**

1130 The data remaining after trimming outlying RTs (5.34%) are displayed in Figure 3 c.
1131 Statistical analyses revealed RT differences between cue conditions, $F(2, 38) =$
1132 $42.72, p < .001, \eta_p^2 = .69$. Fisher's LSD corrected follow-up t-tests showed that all
1133 conditions differed from each other, with faster RTs in 'congruent' than in 'uncued',

1134 $t(19) = 6.21, p < .001$, and 'incongruent' trials, $t(19) = 7.38, p < .001$, and in 'uncued'
1135 than 'incongruent' trials, $t(19) = 5.17, p < .001$.

1136

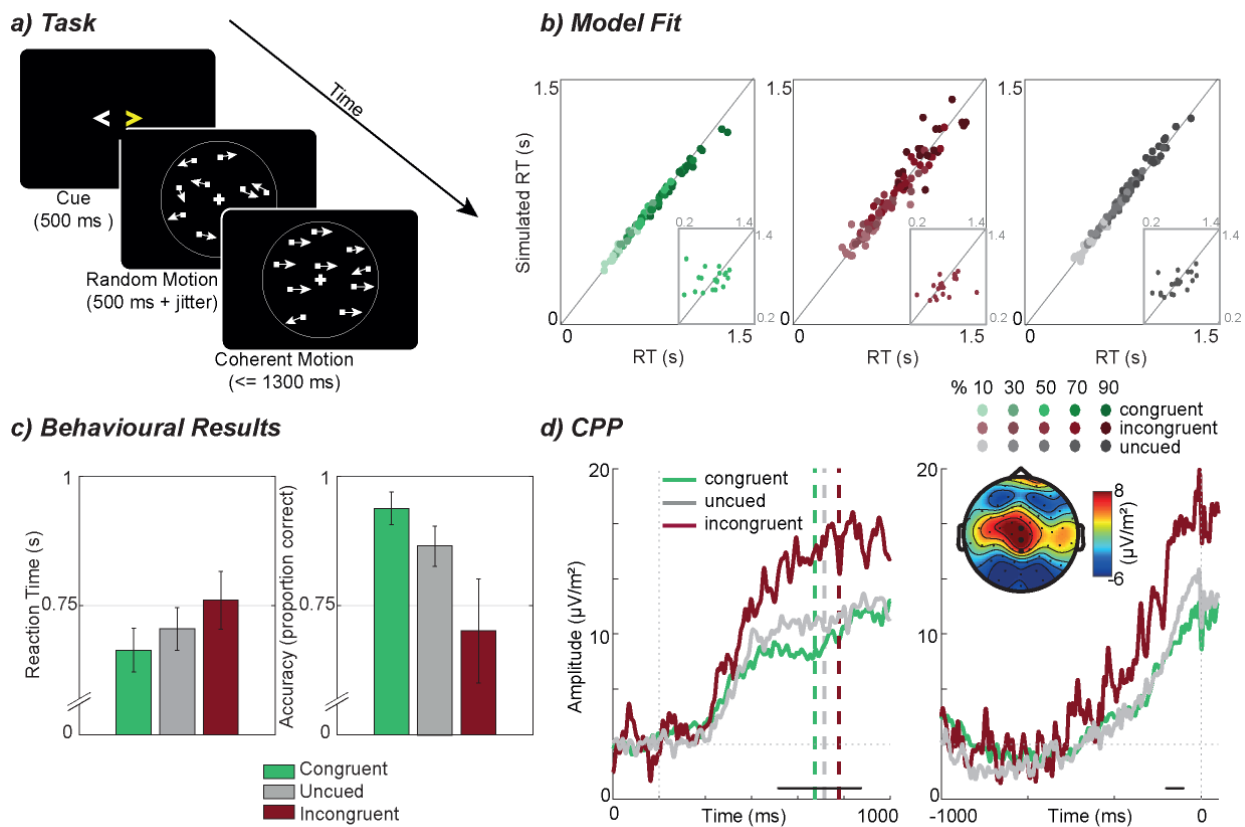
1137 Additionally, a GLMM revealed that the 'Cue' condition affected accuracy scores,
1138 $F(2, 57) = 18.56, p < .001$. To explore the differences between all three levels, we
1139 fitted the model a second time, but setting the reference level of 'Cue' to
1140 'incongruent', rather than 'congruent'. Results showed that accuracy was higher in
1141 'congruent' compared to 'uncued' trials, with both being higher than accuracy of
1142 'incongruent' trials (all $p < .001$).

1143

1144 **3.2.2. ERP Results**

1145 The CPP waveform for each condition is displayed in **Error! Reference source not**
1146 **found.** 3 d. In both the stimulus-locked and the response-locked CPP, the waveform
1147 associated with 'incongruent' trials displays the highest amplitude, followed by the
1148 'uncued' and 'congruent' waveforms. Note that the interpretation of the CPP, when
1149 related to the predictions of sequential-sampling models, requires that we keep in
1150 mind the baseline correction applied to ERPs. Higher end points are consistent with
1151 greater excursions, which may be implemented in models as lower starting points,
1152 and vice versa.

Figure 3



1153

1154 *Figure 3: a) Random dot motion task trial procedure: in each trial, a cue consisting of two arrows was presented.*

1155 *If both arrows were white ('uncued'), no directional information was given. If one of the arrows was yellow, this*

1156 *cue correctly described the direction of the upcoming motion in 80% of trials ('congruent'), and was false in 20%*

1157 *of trials ('incongruent'). Here, the right side is cued, and the coherent motion following the random motion is to*

1158 *the right ('congruent'). Note that the size and number of dots have been adjusted for illustration. b) Model fit: each*

1159 *participant's quantiles estimated from behavioural data (x-axis) and race model simulations (y-axis) for each cue*

1160 *condition (from left to right: congruent, incongruent, uncued). Increasing quantiles (10%, 30%, 50%, 70%, 90%)*

1161 *are represented by increasingly darker colours. Small inserted panels show observed and simulated RT medians*

1162 *for error trials. c) Behavioural results: reaction time (left) and accuracy (right) averages for 'congruent',*

1163 *'incongruent', and 'uncued' trials. Error bars indicate 95% confidence intervals. d) CPP results: Stimulus-locked*

1164 *(left) and response-locked (right) CPP waveforms. Electrodes used to generate the waveforms are highlighted on*

1165 *the topography (which shows the averaged signal over the stimulus-locked 0 to 1000 ms interval). Vertical*

1166 *dashed lines in the stimulus-locked CPP indicate mean RTs per condition. Note that the mean RTs are based*

1167 *only on trials which were included in the generation of the waveform and differ slightly from the ones displayed in*

1168 *c. Black dots at the bottom of the waveform indicate time points at which FDR-controlled comparisons of*

1169 *amplitude showed a significant 'Cue' effect.*

1170 No difference in the CPP slopes was observed across the different conditions, in
1171 either the stimulus-locked, $F(2, 38) = .39, p = .68, \eta_p^2 = .02$, or the response-locked
1172 CPP, $F(2, 38) = .40, p = .67, \eta_p^2 = .02$. We also tested the variation of amplitudes in
1173 the CPP using a series of FDR-controlled ANOVAs and found a significant effect of
1174 'Cue' between 518 and 873 ms relative to the onset of coherent motion (corrected p
1175 $< .049$). Follow-up t-tests revealed that 'incongruent' amplitudes were higher than
1176 both the 'congruent' (for the entire duration of the main effect, corrected $p < .02$), and
1177 the 'uncued' ones (between 542 and 863 ms relative to stimulus onset, corrected $p <$
1178 $.05$). There was less difference between 'congruent' and 'uncued' amplitudes
1179 (corrected $p < .05$ only between 639 and 645 ms).

1180

1181 In the response-locked CPP, we found a significant main effect between -198 and -
1182 104 ms relative to the response (corrected $p < .047$). Post-hoc tests showed the
1183 same patterns as the stimulus-locked data, with higher amplitudes in 'incongruent'
1184 than 'congruent' trials (during the entire duration of the main effect, corrected $p <$
1185 $.018$) and in 'incongruent' than 'uncued' trials (between -198 and -108 ms, corrected
1186 $p < .049$). There was no difference between 'congruent' and 'uncued' trials ($p > .09$).

1187 **3.2.3. Model Fit**

1188 Ten models assuming changes in starting point across bias conditions were fitted to
1189 the data. We once again focussed on BIC to help us discriminate between them. For
1190 individual-level fits, there were no cases where a participant's data were strongly
1191 supportive of one model over all others (BIC or AIC difference > 10). The best
1192 (lowest) group-average BIC was obtained for Model 2, an independent race model
1193 with a symmetrical cuing bias affecting start points of accumulation (see Table 2).
1194 Tukey-corrected contrasts suggested that this model significantly outperformed

1195 models 3, 5 and 10. Without correction, it additionally beat models 1, 4, 8 and 9, but
 1196 not models 6 or 7⁹. This is somewhat suggestive that the additional bias and/or
 1197 inhibition/leak parameters of many of the other models did not increase the quality of
 1198 the fit enough to warrant the increased model complexity. However, model 6, a
 1199 simple LCA model with only a positive cuing bias, performed best based on AIC.
 1200 Somewhat arbitrarily, we begin by discussing accumulation profiles for model 2, but
 1201 go on to consider them for model 6 as the best performer from the other model class
 1202 (for behavioural fits for all models, see Appendix B).

1203

1204 *Table 2: Model Comparison: BIC and AIC values for each independent race (IRA) and LCA model. The BIC and*
 1205 *AIC values of the chosen model (Model 2) are displayed in bold.*

Model	Starting point lower limit	Starting point interval	Response threshold	Accumulation rates	Leak	Inhibition	Non-decision time	Non-decision time interval	Gaussian noise SD	Number of parameters	AIC	BIC
Model 1 (IRA)	Neutral: $Z = 0$ Cued: $Z = bias$ Opp: $Z = 0$	$[Z \ Z+S_z]$	A	V_{corr} V_{inc}	- -	- -	T_{er}	S_{Ter}	σ^2	7	1525	1546
Model 2 (IRA)	Neutral: $Z = bias/2$ Cued: $Z = bias$ Opp: $Z = 0$	$[Z \ Z+S_z]$	A	V_{corr} V_{inc}	- -	- -	T_{er}	S_{Ter}	σ^2	7	1516	1543

⁹ A 2 (model class) x 5 (model details) repeated-measures ANOVA gave little evidence that independent race models were generally better supported than LCA models (with no main effects) for either AIC or BIC, but did yield interactions in both cases.

Model 3	(IRA)	Neutral: $Z = Z$ Cued: $Z = bias$ Opp: $Z = 0$	[Z Z+S _z]	A	V _{corr} V _{inc}	- -	-	-	T _{er}	S _{Ter}	σ ²	8	1515	1547
Model 4	(IRA)	Neutral: $Z = bias/2$ Cued: $Z = bias$ Opp: $Z = 0$	[Z Z+S _z]	A	V _{corr} V _{inc}	V _{cued} V _{cued} * (-1)	-	-	T _{er}	S _{Ter}	σ ²	8	1515	1546
Model 5	(IRA)	Neutral: $Z = Z$ Cued: $Z = bias$ Opp: $Z = 0$	[Z Z+S _z]	A	V _{corr} V _{inc}	V _{cued} V _{opp}	-	-	T _{er}	S _{Ter}	σ ²	10	1516	1556
Model 6	(LCA)	Neutral: $Z = 0$ Cued: $Z = bias$ Opp: $Z = 0$	-	A	V _{corr} V _{inc}	- -	k	β	T _{er}	S _{Ter}	σ ²	8	1513	1545
Model 7	(LCA)	Neutral: $Z = bias/2$ Cued: $Z = bias$ Opp: $Z = 0$	-	A	V _{corr} V _{inc}	- -	k	β	T _{er}	S _{Ter}	σ ²	8	1515	1546
Model 8	(LCA)	Neutral: $Z = Z$ Cued: $Z = bias$ Opp: $Z = 0$	-	A	V _{corr} V _{inc}	- -	k	β	T _{er}	S _{Ter}	σ ²	9	1515	1550
Model 9	(LCA)	Neutral: $Z = bias/2$ Cued: $Z = bias$ Opp: $Z = 0$	-	A	V _{corr} V _{inc}	V _{cued} V _{cued} * (-1)	k	β	T _{er}	S _{Ter}	σ ²	9	1515	1550

Model 10 (LCA)	Neutral: $Z = Z$	-	A	V_{corr}	V_{cued}	k	β	T_{er}	S_{Ter}	σ^2	11	1516	1559
	Cued: $Z = bias$			V_{inc}	V_{opp}								
	Opp: $Z = 0$												

1206
1207

1208

1209 *Table 3: Mean estimated parameter values for the chosen model (Model 2): note that the response threshold A*
 1210 *was set to 1 as a scaling parameter, and that all lower limits of the starting point distributions were generated with*
 1211 *just two free parameters. Note that, due to the raised starting point in the uncued condition, these parameters are*
 1212 *not directly comparable to the ones displayed in Experiment 1 (Table A1).*

Model 2: Parameters

Lower limit starting point	'congruent'	correct	0.2598
		incorrect	0
	'incongruent'	correct	0
		incorrect	0.2598
	'uncued'	correct	0.1628
		incorrect	0.1628
Starting point variability (S_Z)			0.3389
Response threshold (A)			1
Accumulation rate (v)	correct	1.6709	
	incorrect	0.2867	
Non-decision time (T_{er})			0.300
Non-decision time interval (S_{Ter})			0.220
Gaussian noise SD (σ^2)			0.5698

1213
1214
1215

1216

1217 The parameter estimates of the chosen race model are displayed in Table 3.
1218 Figure 3 b shows the quality of the model fit by displaying each participant's
1219 empirical (x-axis) and modelled (y-axis) RT quantiles in each condition. It indicates
1220 that independent race accumulator model 2, with varying starting points, can account
1221 well for our biased decision-making.

1222

3.2.4. Model Prediction (neurodynamics)

1223 Model parameters were used to compute the predicted accumulation profile for each
1224 condition. Figure 4 displays the resulting predictions (b) and the corresponding CPP
1225 (a) for stimulus (left) and response-locked (right) signals. Components of the
1226 prediction (correct and incorrect accumulators) are shown as insets. Visual
1227 inspection shows some qualitative similarities between the best independent race
1228 accumulator model predictions and the EEG signals. Importantly, both the model
1229 prediction and the CPP display an amplitude difference in the response-locked
1230 signal, with 'incongruent' decisions being associated with the highest values.
1231 However, this pattern is not visible in the stimulus-locked prediction, despite
1232 appearing in the corresponding EEG signal. Furthermore, the amplitude variations
1233 appear far more pronounced in the EEG signals than in the model predictions.

1234

1235 As in Experiment 1, we analysed the correlation between differences of conditions in
1236 both the EEG data and the model predictions (differences between 'congruent –
1237 incongruent', 'congruent – uncued', and 'incongruent – uncued', for both stimulus-
1238 locked and response-locked signals, resulting in a total of 6 correlations). We found
1239 that 3 out of 6 tests revealed significant positive correlations, all of which remained
1240 significant after Bonferroni correction ($r_{mean}(98) = .44$, $p_{mean} < .001$). Since this

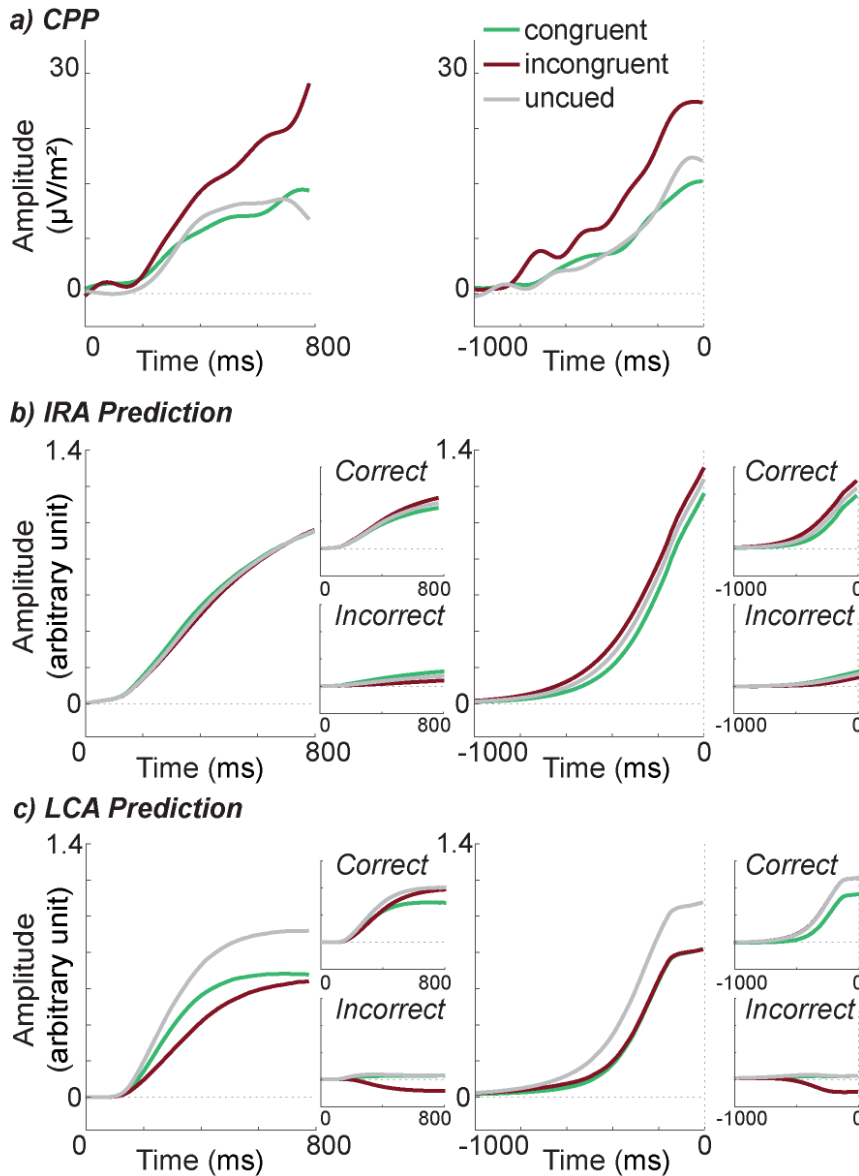
1241 experiment targeted the amplitude of the accumulation, which is visible primarily in
1242 the response-locked profiles, the correlations between response-locked signals,
1243 which were all significant ($r_{mean}(98) = .44, p_{mean} < .001$), are arguably most
1244 meaningful.

1245

1246 Finally, as in Experiment 1, we looked at predictions from the best-performing model
1247 in the alternative class (LCA model 6, Figure 4c). Here, predictions were noticeably
1248 less consistent with the EEG signal. In fact, an identical correlation analysis run on
1249 differences between conditions showed an equal tendency towards both positive and
1250 *negative* significant correlations after Bonferroni correction (three correlations
1251 revealed positive results, $r_{mean}(98) = .46, p_{mean} < .001$, and two showed negative
1252 results, $r_{mean}(98) = -.46, p_{mean} < .001$), i.e. a failure to properly order the EEG signals
1253 from the three conditions across time.

1254

Figure 4



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Figure 4: Decision variable (empirical and simulated): a) CPP waveform for stimulus (left) and response-locked (right) data. The CPP here has been filtered and downsampled to match model predictions. b) Accumulation profile per cue condition as predicted by the best-fitting independent race accumulator model (IRA), for stimulus (left) and response-locked (right) data. Correct and incorrect accumulators were summed to form the prediction, so these contributory signals are shown separately as smaller insets. c) Accumulation profile as predicted by the best-fitting LCA model. Details as in part b.

1263 **3.3. Discussion Experiment 2**

1264 In Experiment 2, we tested how decision biases affect the CPP waveform and, like in
1265 Experiment 1, compared its profile to model predictions. To this end, we asked
1266 participants to complete a motion discrimination task in which cues prior to each trial
1267 either gave no information about the direction of the upcoming trial ('uncued'), or
1268 indicated the upcoming direction either correctly ('congruent') or incorrectly
1269 ('incongruent'). In accordance with previous research (de Lange et al., 2013; Mulder
1270 et al., 2012; Teodorescu & Usher, 2013), we observed that participants' choices
1271 were biased towards the cued direction. Compared to 'uncued' trials, 'congruent'
1272 cues resulted in faster RTs and less errors, while 'incongruent' cues led to lower
1273 accuracy and longer RTs. Note that in order to avoid the co-occurrence of visual
1274 evoked potentials (associated with a sudden stimulus onset) with the accumulation
1275 profile, we added a period of random dot motion prior to the coherent motion but
1276 following the directional cue (Figure 3 a). This means that there was a short period of
1277 time where participants were presented with a stimulus which was potentially
1278 inconsistent with the cue, even in congruent trials, which may have weakened the
1279 effect of the cue. However, since we observed strong behavioural differences
1280 between all three conditions, we do not believe that this had a qualitative impact on
1281 our conclusions. Nevertheless, we note that this may hinder the direct comparison
1282 with versions of decision-making tasks in which the evidence immediately follows the
1283 cue.

1284 The observed changes in behaviour were well captured by an independent race
1285 model with varying start points, and this model predicted some of the trends we
1286 observed in the CPP as decisions were being made, albeit imperfectly. However, this
1287 result may be viewed as somewhat fortuitous. Although generating predictions for

1288 the independent race model followed a natural logic, because this model (just about)
1289 won at a behavioural level, the other class of models we considered here, with
1290 inhibition and leakage, failed to capture nuances in the CPP.

1291

1292 Based on previous research, we hypothesised that prior cues would affect the
1293 starting point of each accumulator (Bode et al., 2012; Gao et al., 2011; Rorie et al.,
1294 2010; Teodorescu & Usher, 2013) leading to a change in the baseline-to-threshold
1295 distance, and incorporated free parameters capable of capturing this change. For the
1296 best-fitting model, the mean starting point was higher in the corresponding cued
1297 accumulator and lower in the opposite non-cued accumulator compared to the
1298 neutral, uncued, condition. By modifying the baseline-to-threshold distance, starting
1299 point variations affect both the time required for accumulation to reach the decision
1300 threshold and the probability of attaining the threshold due to noise. In incongruent
1301 trials, for example, where the incorrect response was cued, errors occurred
1302 frequently due to the small baseline-to-threshold distance in the cued, but incorrect,
1303 accumulator, and correct RTs were slower due to the larger baseline-to-threshold
1304 distance in the opposite non-cued accumulator¹⁰. In line with many, but not all,
1305 previous studies, our results hence confirmed that decision biases can be accounted
1306 for by simply varying accumulation starting point (Basso & Wurtz, 1998; de Lange et
1307 al., 2013; Rao et al., 2012; but see Rae et al., 2014).

1308

¹⁰ In the case of the best LCA model, which incorporated a change to only the cued starting point, correct RTs would instead be slower due to the extra inhibition flowing from the boosted correct accumulator towards the non-cued accumulator.

1309 The exact pattern these changes would evoke in the CPP waveforms however is
1310 difficult to predict intuitively. Firstly, due to the baseline correction applied to compute
1311 the CPP waveform, a starting point difference would not be observed directly, but
1312 would instead lead to a difference in amplitude, with higher starting points leading to
1313 lower ERP peaks. Secondly, and as confirmed by model parameters, prior cues
1314 induced both an increased accumulation starting point for the cued response, and a
1315 decreased starting point for the non-cued response. Since the EEG signal recorded
1316 from the scalp is the sum of all underlying neural activities, the CPP presumably
1317 reflects the sum of all accumulation in a race model. It is hence unclear how opposite
1318 effects on the activity of 'correct' and 'incorrect' accumulators affects the global
1319 activity amplitude. There are a number of possible outcomes which could, at least
1320 conceptually, be considered in line with sequential sampling models. It is therefore
1321 particularly important to directly compare a signal to predictions made through model
1322 fits, in order to comment on its similarity to an accumulation process. However, it is
1323 worth bearing in mind that the relative nature of the CPP may make it an inherently
1324 less informative signal (relative to single-cell firing rates, with meaningful zero points)
1325 for the evaluation of experimental manipulations affecting the start point of
1326 accumulation.

1327

1328 The pattern we observed in the CPP was somewhat similar to what might be
1329 expected for just a correct accumulator. We found a clear difference in amplitude
1330 between the conditions, but no difference in slope. The waveform associated with
1331 'incongruent' decisions showed a greater excursion than 'congruent' or 'uncued'
1332 profiles in both the stimulus and the response-locked data. The 'uncued' CPP also
1333 seemed to build up to a slightly higher plateau than the 'congruent' waveform,

1334 although this difference was not significant in our analysis. However, it is difficult to
1335 conceive how a non-lateralised EEG signal could represent only one accumulator –
1336 only a sum, or perhaps absolute difference of accumulators makes sense. In order to
1337 evaluate to what extent this observed CPP pattern resembled the sum of
1338 accumulation processes as predicted by sequential sampling models, we simulated
1339 accumulation profiles predicted in each condition, based on the estimated
1340 parameters of the best-fitting (independent race) model. The resulting waveforms
1341 showed that all three conditions are predicted to follow a very similar trajectory, but
1342 do differ slightly in amplitude. For response-locked signals, the order in which the
1343 amplitudes differ is identical to the one described by the CPP, with the highest
1344 amplitude seen for ‘incongruent’ decisions, followed by ‘uncued’ decisions, and
1345 ‘congruent’ waveforms showing the lowest amplitude.

1346

1347 Although both the (race-model) simulated accumulation profiles and the CPP display
1348 similar patterns, it is not immediately clear what caused them. As outlined above,
1349 while we expected this pattern for the correct accumulator, summing over the
1350 accumulators would presumably cancel differences between the conditions. To aid
1351 our interpretation, we explored the accumulation profiles in more detail. First, we
1352 found that dividing correct and error trials had an impact. In Figure 4, only correct
1353 trials are averaged to match with the CPP analysis. However, in the incongruent
1354 condition in which the mean starting point is higher in the incorrect accumulator,
1355 correct trials are primarily trials in which noise has favoured the correct accumulator,
1356 such as trials in which, by chance, the cued incorrect starting point was at the lower
1357 limit of the distribution, leading to a larger baseline-to-threshold distance.

1358

1359 Nonetheless, averaging the accumulation profiles over all correct and error trials still
1360 resulted in a pattern qualitatively similar to the one for correct trials alone, indicating
1361 that some additional mechanism/s must help generate the observed differences.
1362 Inspecting correct and incorrect accumulation traces separately (see figure insets)
1363 confirmed that starting-point differences resulted in opposing amplitude modulations
1364 in correct and incorrect accumulators. For correct accumulation, the highest
1365 amplitude was obtained for incongruent trials, and the lowest trace in congruent
1366 trials. The reversed pattern was observed in the incorrect accumulator. However,
1367 differences between conditions were more pronounced on correct than incorrect
1368 traces, particularly in response-locked signals. We presume that this divergence
1369 arises from the accumulation rate difference between the accumulators, which
1370 implies that correct accumulation is less affected than incorrect accumulation by
1371 noise. Accordingly, incorrect traces are flatter overall and diverge less between
1372 conditions, such that differences in the correct accumulator contribute more to the
1373 summed signal.

1374

1375 Regardless of the computational specifics that generate differences between our
1376 conditions, the CPP and the simulated accumulation profiles display somewhat
1377 similar patterns, suggesting similar underlying mechanisms, and supporting the role
1378 of the CPP as an accumulation signal, at least when certain classes of model are
1379 used to describe the decision process. Furthermore, these findings again emphasise
1380 the importance of a direct comparison between the CPP and model predictions, as
1381 the patterns reported here are difficult to predict based on intuitive reasoning alone.
1382 However, it is also clear that our conclusion was dependent on the models we
1383 included, and on the particular model that won at a behavioural level (although we

1384 gave our models no capacity to adjust to the neurodynamic data, a point we return to
1385 in the general discussion).

1386

1387 Our findings also contrast in some respects with a very recent but highly relevant
1388 CPP study, investigating the effect of a decision bias induced through manipulating
1389 the reward value of different choices under extreme time pressure (Afacan-Seref et
1390 al., 2018). Their overall conclusion is similar to ours – both studies successfully
1391 modelled RTs via sequential sampling, and showed correspondence between
1392 predicted accumulation profiles and the CPP. However, their data supported a non-
1393 standard model incorporating sensory-level dynamics (a linearly increasing
1394 accumulation rate for a constant stimulus) and a bias affecting accumulation rates
1395 rather than starting points (leading to an initially negative relative accumulation rate
1396 for a low valued but strongly evidenced choice). We did not test such a model, which
1397 may have specific relevance in their somewhat unusual experimental context. The
1398 extreme time pressure used in their experiment is likely to influence the decision
1399 dynamics, as the urgency of the choice may accelerate the accumulation in a way
1400 that is qualitatively different from the decisions made in our experiment. In any case,
1401 we make no claims that the model we have fitted and illustrated predictions from is
1402 the only (or best) possible implementation. We do, however, argue that it is a
1403 plausible choice, and one that is consistent with both the behaviour and, to some
1404 extent, the neurodynamics that we observed.

1405

1406 **4. General Discussion**

1407

1408 Model-based cognitive neuroscience, which combines the analysis of neural data
1409 with mathematical modelling, has gained momentum in recent years. However, the
1410 field of human perceptual decision-making has oftentimes not made full use of this
1411 approach. Here, we aimed to explore decision-related evidence accumulation in the
1412 human brain by directly comparing predictions made by different behavioural models
1413 to the dynamics of the CPP. The CPP is a centroparietal ERP component which has
1414 previously been suggested to display decision-related accumulation of evidence
1415 independent of sensory and motor processes (Kelly & O’Connell, 2013; O’Connell et
1416 al., 2012; Twomey, Kelly, & Connell, 2016). We aimed not only to explore the effect
1417 of previously untested manipulations on the CPP, but also to evaluate the resulting
1418 waveforms using sequential sampling modelling. Neural correlates of accumulation
1419 are often evaluated by deriving summary measures, such as slope of accumulation,
1420 and comparing them with expectations made with reference to sequential sampling
1421 models. However, the dynamics of even simple models are difficult to intuit. We
1422 therefore used sequential sampling models to fit the behavioural data and compared
1423 neural data to the predicted accumulation profiles based on the estimated
1424 parameters. The CPP showed a marked degree of correspondence with certain
1425 model predictions – perhaps fortuitously, the very predictions made by the models
1426 which best explained the behavioural data in each experiment.

1427

1428 In Experiment 1, we investigated the impact of non-stationary evidence on the CPP
1429 waveform, under the assumption that changing evidence should affect evidence
1430 accumulation dynamics. In Experiment 2, we explored the impact of decision bias on
1431 CPP patterns. We expected that decision biases induced by predictive cues would
1432 result in shifts of accumulation starting points, hence changing the baseline-to-

1433 threshold distance. In both experiments, we observed the anticipated behavioural
1434 changes. Furthermore, sequential sampling model fits confirmed that accumulation
1435 rates were affected during evidence interruption, while starting point shifts could
1436 account for decision biases effects. It is worth noting however that when considering
1437 only behavioural data (for which free parameters in the models could be tuned to
1438 enhance goodness of fit), Experiment 1 and Experiment 2 supported two different
1439 model architectures. While a simple independent race accumulator model provided
1440 the best fit to biased decision data, the LCA model was superior in the case of non-
1441 stationary evidence, although in neither case were the differences between models
1442 entirely compelling.

1443

1444 We believe that this apparent discrepancy might be explained by the nature of each
1445 task manipulation, and the universal preference for simpler models. This preference
1446 is expressed in goodness-of-fit indices such as BIC or AIC by penalising models for
1447 a higher number of model parameters. Simple independent race models may
1448 therefore be favoured compared to the more complex LCA (which has a similar basic
1449 architecture but additional parameters to capture plausible physiological processes),
1450 especially in the case of fast RTs as observed in Experiment 2, in which the
1451 influence of inhibition and leakage may be limited. Conversely with longer decisions,
1452 especially associated with dynamical modulations of each accumulator's activity as
1453 in Experiment 1, both reciprocal inhibition and leakage potentially play an important
1454 role. In this case, a model incorporating these phenomena may be preferred. In other
1455 words, inhibition and leakage may always be present to some extent, but including
1456 these parameters in the decision models improves model fit only when decisions are

1457 slow and potentially more sensitive to interactions between accumulators¹¹. Indeed,
1458 in some cases, patterns of behavioural data emerge which seem to demand the
1459 inclusion of parameters capturing crosstalk between accumulators. For example, we
1460 have recently found that when up to four manual actions are instructed by a stimulus
1461 (left/right hand pinch/power grip responses), gross differences in error rates emerge
1462 based purely on the anatomical adjacency of responses (i.e. without any correlate in
1463 the stimulus; Kohl, Spieser, Forster, Bestmann, & Yarrow, 2019).

1464

1465 Experiments 1 and 2 were designed to be complementary, because the two types of
1466 manipulation tested two different predictions about the decision process, each
1467 realised as a different aspect of evidence accumulation. In Experiment 1, we used
1468 non-stationary evidence to affect the accumulation process. In their initial CPP
1469 description, O'Connell et al. (2012) observed that the CPP was susceptible to a
1470 change in evidence. Our results confirmed that the CPP profile is affected by a time-
1471 varying input, a necessary feature of a signal which could reflect the accumulation of
1472 evidence, and extended this result to choice-RT settings. While continuous evidence
1473 led to a gradual build-up of the CPP waveform, interrupted evidence caused a
1474 disruption in this build-up. Surprisingly, the two different interrupted conditions, one
1475 in which evidence was stopped, and one in which evidence was reversed, gave rise
1476 to very similar waveforms, even though they were associated with different
1477 behavioural patterns. Nevertheless, the pattern of the CPP closely resembled our
1478 best-fitting model predictions. In other words, our LCA model, combined with realistic

¹¹ Another perspective would be that these models are all describing the same fundamental model architecture, but with certain strategies requiring additional parameters, as when a non-stable environment demands the presence of leak parameters to discount the past (Kilpatrick, Holmes, Eissa & Josić, 2019).

1479 assumptions about the origin of the CPP signal, successfully predicted the *absence*
1480 of an effect that might have been expected based on intuition alone.

1481

1482 In Experiment 2, we used predictive cues to manipulate decision biases. Previous
1483 research mainly suggests that biases affect the starting point of accumulation, with
1484 the resulting effect on the EEG signal requiring further clarification (Bode et al., 2012;
1485 Gao et al., 2011; Rorie et al., 2010, but see Afacan-Seref et al., 2018). We found that
1486 the CPP differed in amplitude across bias conditions. In particular, decisions in which
1487 a directional cue was incongruent with subsequent motion were associated with
1488 higher amplitudes than both decisions in which the cue was congruent with the
1489 motion and decisions in which there was no directional cue. Once again, a
1490 sequential sampling model was able to account for all behavioural data, in this case
1491 by varying the starting points across bias conditions. Furthermore, for the best-fitting
1492 independent race model, both real and model-predicted EEG signals displayed a
1493 pattern in which profiles associated with different bias conditions differed only in
1494 amplitude, with decisions with incongruent cues showing the highest amplitude,
1495 followed by uncued decisions, and trials with congruent cues showing the lowest
1496 amplitude, at least for response-locked signals. Hence here, an independent race
1497 model successfully predicted the presence of an effect that might *not* have been
1498 predicted intuitively. The simulations revealed that these differences in amplitude
1499 were not strictly the result of baseline differences, which in fact largely cancelled out
1500 on average, but were instead caused by mechanisms such as a biased
1501 representation of variability parameters in correct trials, or interactions between
1502 accumulation rate and noise parameters.

1503

1504 However, a problematic feature of our results emerges when looking across
1505 experiments. In our first experiment, an LCA model best fitted the behavioural data,
1506 and provided a good match to the CPP. A simpler independent race model was
1507 slightly less successful, but nonetheless showed qualitative agreement on both
1508 counts. In Experiment 2, an independent race model best fitted the behavioural data,
1509 and provided a reasonable match to the CPP. However, the more complex LCA
1510 model failed to predict the precise ordering of conditions in the CPP signal. What are
1511 we to conclude across both experiments?

1512

1513 When considering this disparity, we would emphasise that our approach gave the
1514 models leeway to fit the behavioural data, but not the CPP. By exploiting free
1515 parameters to capture nuances (and even noise) in the behavioural data, models
1516 may end up producing neurally unrealistic accumulation patterns. The approach we
1517 apply here has some clear strengths – by fitting only to behaviour, a model’s success
1518 in predicting the associated neurodynamics becomes all the more striking, because
1519 no flexibility is provided for achieving this match (a situation somewhat akin to cross
1520 validation, but on a second form of data). However, it is only one of several ways in
1521 which model-based cognitive neuroscience might be applied (see e.g. Turner,
1522 Forstmann, Love, Palmeri, & Van Maanen, 2017, for discussion) and it is not clear
1523 whether a subsequent comparison of models on this (unfitted) neurodynamic data is
1524 a fair one. If we accept that signals like the CPP do indeed represent evidence
1525 accumulation, an important goal for future research will be to produce a consensus
1526 method for simultaneously fitting models to both RT and EEG data (cf. Turner et al.’s
1527 “integrative” approach). This is by no means trivial, because EEG data are

1528 autocorrelated (to an uncertain extent) which greatly complicates the estimation of
1529 likelihood when matching model predictions to data.

1530

1531 In fact, one might argue that our observation here, that specific sequential sampling
1532 models can predict the CPP under a particular manipulation, but that a single model
1533 may not apply under different manipulations, is the norm in a fragmented literature.

1534 Thus far, where specific models have been compared to the CPP in terms of the full
1535 time-varying profile of accumulation, researchers have tended to capture only a
1536 small subset of possible manipulations. For example, a difficulty manipulation has
1537 been modelled via a drift-diffusion model (Twomey et al., 2015); a speed-accuracy
1538 trade-off has been captured via a (reconfigured) race model (Spieser et al., 2018),
1539 albeit with an unusual take on how the brain might implement this strategic
1540 adjustment; and value-based biasing under extreme time pressure has been
1541 modelled via an accelerating accumulation model (Afacan-Seref et al., 2018).

1542 Whether one views the primary question as “does the CPP represent evidence
1543 accumulation”, or, having accepted this predicate, as “which model best captures
1544 both behaviour and neurodynamics”, it seems clear that finding a single (class of)
1545 model(s) that explains the CPP across multiple experimental manipulations should
1546 be of central concern in future research.

1547

1548 In line with research which is increasingly emphasising the advantages of combining
1549 behavioural data, mathematical modeling, and neural dynamics (Ditterich, 2010;
1550 Forstmann et al., 2011; Mulder et al., 2014; Purcell & Palmeri, 2017), our findings
1551 also highlight the importance of combining behavioural modeling and neuroimaging

1552 methods and directly comparing the dynamics of the neural signals and the model
1553 predictions, as neither are easily predictable based on conceptual reasoning alone.
1554 Despite the substantial similarity between the CPP and the predicted accumulation
1555 profiles observed here, there were also differences worth noting. For example, in
1556 Experiment 2, the amplitude differences between the conditions are far more
1557 pronounced in the CPP than in the model predictions even in the response-locked
1558 signals. This is likely to represent some degree of error in either our choice of
1559 models or assumptions regarding exactly how accumulators combine to form the
1560 CPP (something about which there is currently no consensus). However, it is
1561 important to note that the CPP is unlikely to ever replicate model predictions exactly
1562 for a number of reasons. Firstly, any model can, at best, be an approximation of true
1563 biological processes. A second reason for differences between the CPP and the
1564 model predictions lies in the nature of EEG recordings. EEG is measured from the
1565 scalp and can only record the sum of all electrical activity underneath each
1566 electrode, which has presumably been subject to complex filtering by intervening
1567 biological substrates. Furthermore, since the brain is constantly performing
1568 computations unrelated to accumulation, the signal-to-noise ratio is low. Most of
1569 these computations are unlikely to be time-locked to the decisions and are therefore
1570 averaged out, and the impact of conducted activation from more distal sources is
1571 reduced using the current source density transform which increases the spatial
1572 selectivity of the data. Nevertheless, noise and systematic distortions likely remain.
1573 For reasons like these, the degree of similarity between the CPP and predicted
1574 accumulation profiles derived from a class of models originally intended to predict
1575 only behaviour remains remarkable.

1576

1577 **4.1. Conclusions**

1578 In summary, we provide further support for the role of the CPP as a neural substrate
1579 of the decision variable, but also highlight how researcher flexibility regarding which
1580 models to consider and apply might give a false degree of assurance on this front.
1581 We have shown that the CPP is sensitive to two manipulations which influence
1582 decision-making behaviour, namely non-stationary evidence and decision biases.
1583 Importantly, we fitted sequential sampling models to the behavioural data and
1584 simulated the resulting accumulation profiles. We found that the CPP waveform
1585 resembled the modelled accumulation in important ways when models were selected
1586 in a principled, but perhaps somewhat fortuitous, manner. In our opinion, the CPP
1587 probably reflects the accumulation of evidence and remains a highly plausible
1588 correlate of the decision variable. Indeed, it may now be time to move beyond mere
1589 validation of the CPP, to a point where we can instead use it as an additional metric
1590 to help differentiate competing models of speeded choice.

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1592

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1874

1875 **Appendix A**

1876 Parameter identifiability issues have been reported in the LCA model (Miletić et al.,
 1877 2017). Hence, we conducted a recovery study to assess the accuracy of parameter
 1878 estimation in Experiment 1. The mean parameter estimates of the chosen LCA
 1879 model (Model 5, LCA-symmetric with no delay) are displayed in Table A1¹². Based
 1880 on this model, we simulated 20 RT datasets with all 3 interruption conditions and 2
 1881 difficulty levels. We simulated 160 trials in each condition, leading to 960 trials in
 1882 total (i.e., corresponding to the size of one participant’s RT data). Parameters values
 1883 for each of the 20 simulated datasets were drawn from a uniform distribution around
 1884 mean empirical values.

1885

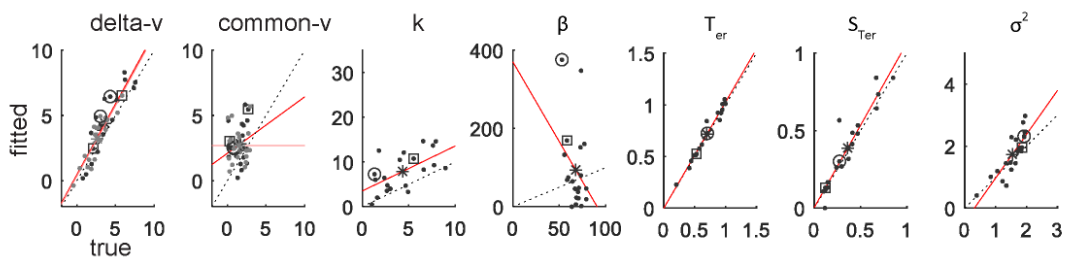
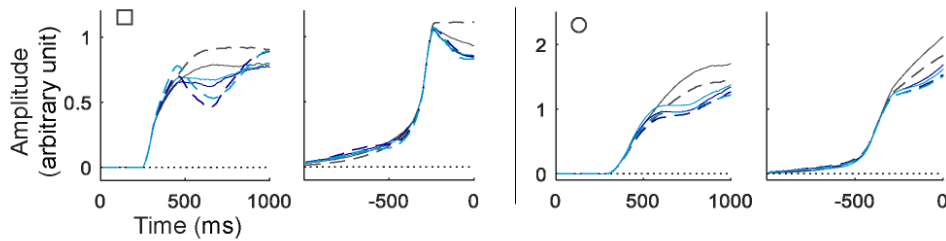
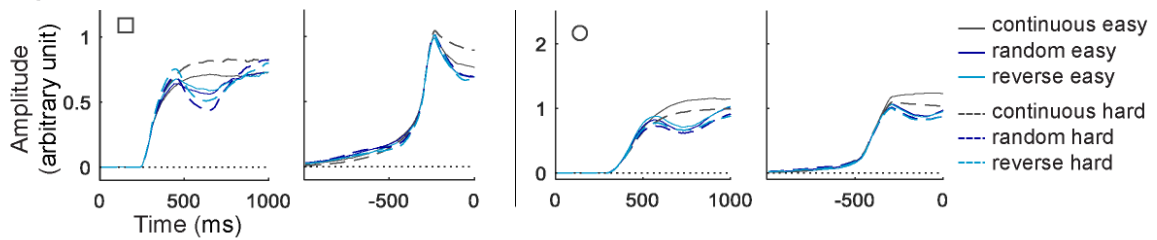
1886 *Table A1: Mean estimated parameter values for the chosen model (Model 5), note that the response threshold A*
 1887 *was set to 1 as a scaling parameter.*

Model 5: Parameters			
Decision threshold (A)			1
Accumulation rate (v)	easy	correct	6.0154
		incorrect	1.4110
	hard	correct	5.0199
		incorrect	1.5039
Leakage (k)			5.2706
Inhibition (β)			65.7646
Non-decision time (T_{er})			0.3574
Non-decision time interval (S_{Ter})			0.2763

¹² Parameter values are only comparable across studies if the same scaling parameter is used. Here we fixed the decision threshold but let noise vary, yielding a larger than typical Gaussian noise SD (and thus amplified values for many parameters).

1888

1889

Figure A1**a) Parameter Recovery****b) True Parameters****c) Fitted Parameters**

1890

1891 *Figure A1: a) Parameter recovery: fitted parameter values as a function of true values, for 20 simulations of*1892 *individual RTs. Dots show the 20 individual fit values and asterisks show mean fitted value as a function of mean*1893 *true value. Dotted lines show ideal recovery of fitted from true parameters. Red lines show linear regressions*1894 *between true and fitted values. Rate parameters are decomposed in delta-v and common-v (see details in text),*1895 *and both easy (dark) and hard (light) conditions are shown. Circles and squares identify parameter sets used*1896 *to compute predictions in b and c. b) and c) CPP predictions for 2 sets of parameters, computed based on true*1897 *values (b) and fitted values (c). Both parameters sets are identified in a) by circles (predictions on left panel) and*1898 *squares (predictions on right panel). Stimulus-locked (left) and response-locked (right) predictions are shown.*

1899

1900 Figure A1 shows the obtained fitted values as a function of true values for each

1901 parameter. Note that accumulation rates are decomposed into *delta-v* and *common-*

1902 v , corresponding respectively to the difference and the common components of
1903 correct and incorrect rates (i.e., $\text{delta-}v$ equals v_{corr} minus v_{inc} , and $\text{common-}v$ equals
1904 v_{inc}). Ideally, values recovered from the fit would equal the true parameters, falling on
1905 the black dotted line. Red lines show best-fitting linear regressions between true and
1906 fitted parameter values. To assess the accuracy of parameter estimation at a group
1907 level, we also represented the average of fitted values as a function of the mean true
1908 value. Consistent with a previous report (Miletić et al., 2017), we observed good
1909 recovery for $\text{delta-}v$, T_{er} and σ^2 , as well as $S_{T_{\text{er}}}$, and poor recovery for $\text{common-}v$, k
1910 and β parameters. At the group level, however, the mean fitted parameter values
1911 were still a good estimation of mean true values (asterisks in Figure A1a).

1912

1913 Finally, and critically, in order to assess the impact of parameter estimation accuracy
1914 on derived CPP predictions, we computed predictions based on true and fitted
1915 parameters values. Predictions are shown for two sets of parameters in Figure A1.
1916 They have been selected as being both representative of our general findings
1917 (across all 20 simulations) and illustrative of cases where recovered parameters
1918 appear to have traded off, and thus differ from true parameters. As can be seen, the
1919 global pattern is retrieved in fitted parameter predictions, even in those cases where
1920 $\text{common-}v$ and β parameters were not estimated accurately.

1921

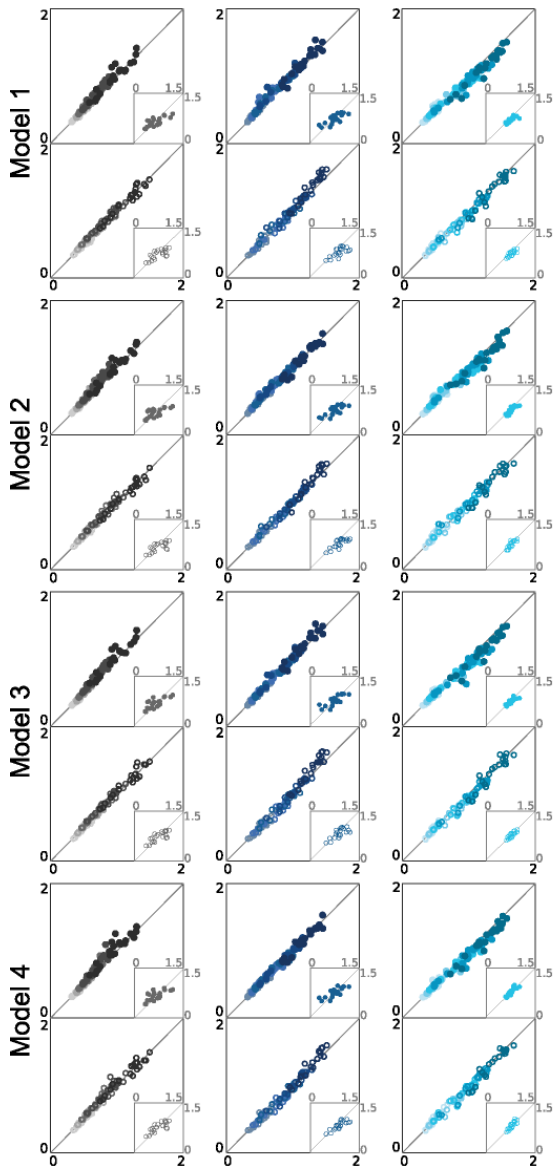
1922 **Appendix B**

1923 In both experiments, many of the models performed somewhat similarly. For
1924 completeness, the behavioural fits of all models are displayed in Figures B1
1925 (Experiment 1, see Figure 1 b), and B2 (Experiment 2, see Figure 3 b).

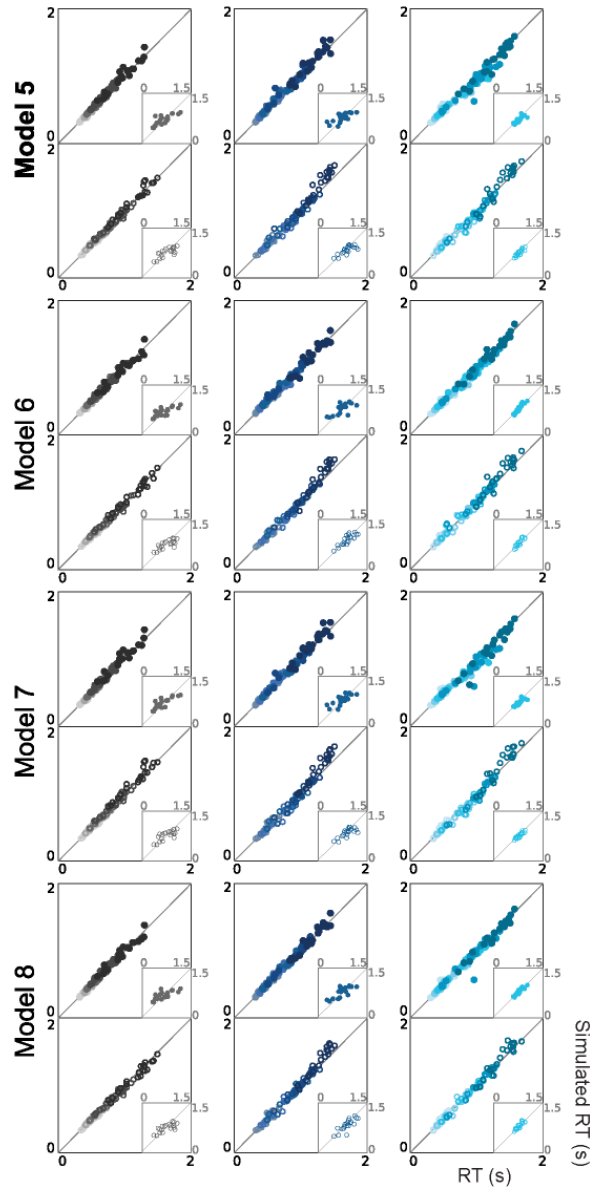
1926

Figure B1

a) IRA



b) LCA



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1930

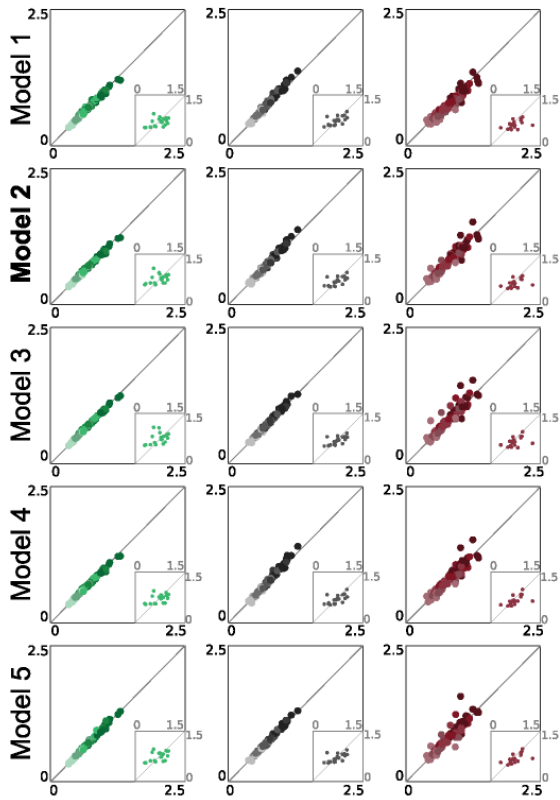
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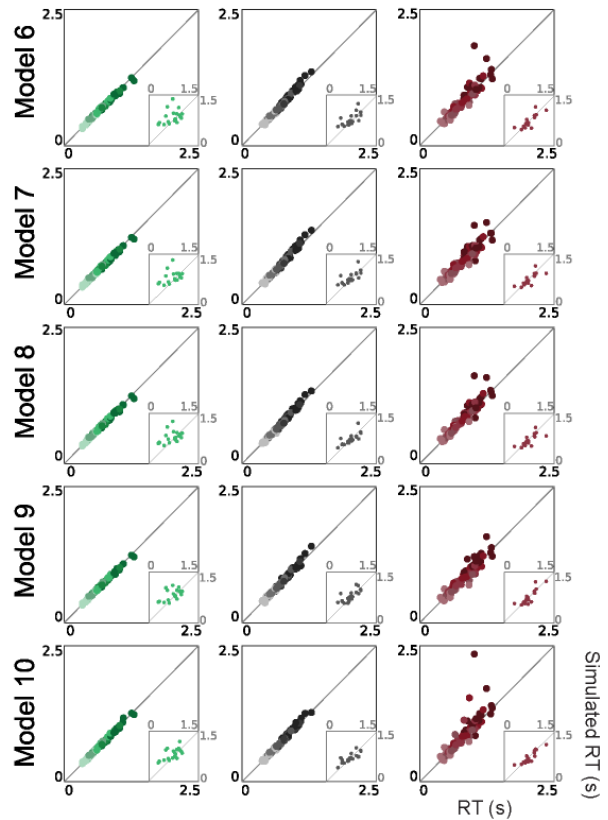
Figure B1: Experiment 1, Behavioural fits for all models: RT quantiles from behavioural data (x-axis) and simulations (y-axis) in seconds for each independent race (IRA, 1 to 4) and LCA (5 to 8) model for easy (filled circles, top rows) and hard (empty circles, bottom rows) decisions. Small inserted panels show observed and simulated RT medians for error trials.

Figure B2

a) IRA



b) LCA



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1934

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1936

1937

Figure B2: Experiment 2, Behavioural fits for all models: RT quantiles from behavioural data (x-axis) and simulations (y-axis) in seconds for each race (IRA, 1 to 5) and LCA (6 to 10) model. Small inserted panels show observed and simulated RT medians for error trials.