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Second Guessing in Perceptual Decision-Making

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Authors

McLean, Charlotte S Ouyang, Bowen Ditterich, Jochen

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3	Authors: Charlotte S. Mc		cLean ^{1,2} , Bowen Ouyang ^{1,2} and Jochen Ditterich ^{1,3}
4		¹ Center for Neu	uroscience and Dept. of Neurobiology, Physiology & Behavior,
5		University of C	alifornia, Davis, Davis, CA 95618
6		² These authors	s have contributed equally to this work.
7		³ Corresponding	g author: jditterich@ucdavis.edu
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21 ABSTRACT

22 Human subjects of both sexes were asked to make a perceptual decision between multiple directions of 23 visual motion. In addition to reporting a primary choice, they also had to report a second guess, 24 indicating which of the remaining options they would rather bet on, assuming that they got their 25 primary choice wrong. The second guess was clearly informed by the amounts of sensory evidence that 26 were provided for the different options. A single computational integration-to-threshold model, based 27 on the assumption that the second guess is determined by the rank ordering of accumulated evidence at 28 or shortly after the time of the decision, was able to explain the distribution of primary choices, 29 associated response times, and the distribution of second guesses. This suggests that the decisionmaker 30 has access to how well supported unchosen options are by the sensory evidence.

31

32 SIGNIFICANCE STATEMENT

33 Perceptual decisions require conversion of sensory evidence into a discrete choice. Computational 34 models based on the accumulation of evidence to a decision threshold can explain the distribution of 35 choices and associated decision times. Subjects are also able to report the level of confidence in their 36 decision. Here we show that, when making decisions between more than two alternatives, the 37 decisionmaker can even report a second guess that is clearly informed by the sensory evidence. These 38 second guesses show a distribution that is consistent with subjects having access to how much sensory 39 evidence was accumulated for the unchosen options. The decisionmaker therefore has knowledge about 40 the outcome of the decision process that goes beyond just the choice and an associated confidence.

41

43 INTRODUCTION

44 Perceptual decisions require a decisionmaker to make a discrete choice on the basis of sensory 45 information. Substantial work has gone into elucidating the mechanisms that allow the inflowing 46 sensory evidence to be converted into a discrete choice. Integration-to-threshold mechanisms are the 47 currently dominant class of models, the Drift Diffusion Model (DDM) being a popular exemplar (Luce, 48 1986; Ditterich, 2006; Ratcliff and McKoon, 2008; Ditterich, 2010; Forstmann et al., 2016). These models 49 are based on the idea that sensory evidence for each available option is accumulated until the 50 accumulated evidence for one of the options exceeds a decision threshold. They can explain the 51 distribution of choices and associated response times (RTs) for a wide range of decision tasks (Ratcliff 52 and Smith, 2004) and are consistent with decision-related neural activity, both averaged across trials as 53 well as on a single-trial level (Ditterich, 2006; Bollimunta et al., 2012). It is difficult, however, to pinpoint 54 experimentally how much temporal integration is involved in the process (Ditterich, 2006), and the view 55 that single-trial decision-related neural activity is consistent with a diffusion-like process has been 56 challenged (Latimer et al., 2015). 57 More recently, confidence in a perceptual decision has become the focus of scientific investigation. 58 Some studies suggest that a common mechanism could explain both the outcome of the decision as well 59 as the reported confidence (Kiani and Shadlen, 2009; Kiani et al., 2014), while other reports have

60 focused on dissociations between subjective confidence and objective decision accuracy (see Rahnev

and Denison (2018) for a review). When making binary decisions, the choice and the associated

62 confidence fully describe the outcome of the decision process. When making decisions between more

than two alternatives, the decisionmaker could also have knowledge about how well the sensory

64 evidence supported the unchosen options.

65 Here we ask whether human subjects have access to information about the "relative desirability" of the 66 unchosen options when making perceptual decisions between more than two alternatives and, if so, 67 whether one can provide a quantitative explanation for the distribution of reported second guesses. We 68 used a modified version of the 3-alternative forced choice (3AFC) version of the multi-component 69 Random Dot Motion (RDM) direction discrimination task introduced in Niwa and Ditterich (2008). 70 Briefly, the subject watches an RDM stimulus that simultaneously contains coherent motion in three 71 different directions, all separated by 120 deg. The strength of each motion component is chosen 72 randomly. The observer has to determine the strongest motion component and indicate its direction 73 with an eye movement. The choice and the associated RT are recorded. For this study, subjects were 74 instructed to also report a second guess with a second eye movement. We asked the observers to 75 indicate which of the remaining two options they would rather bet on, assuming they got their primary 76 choice wrong. Once both the primary choice and the second guess had been registered, auditory 77 feedback about the accuracy of the primary choice was provided. Subjects did not receive feedback on 78 their second guess. The task is illustrated in Figure 1. Further details regarding the experimental design 79 can be found in Materials and Methods.

Here we demonstrate that the second guess is clearly informed by the sensory evidence and that a single integration-to-threshold model can explain the distribution of primary choices, associated RTs, and the distribution of second guesses. This suggests that the decisionmaker has access to how much sensory evidence had been accumulated for options other than the chosen one at the time when the decision was made. We also consider alternative models and show that the second-best explanation for the data is provided by a model that starts a new decision process between the remaining alternatives when the primary decision is made and reads out the decision variable after a fixed amount of time.

87

88

89 MATERIALS AND METHODS

90 Experimental Design and Statistical Analyses

91 Human Subjects

92 The study was approved by the UC Davis Institutional Review Board. After giving their informed consent, 93 seven UC Davis undergraduate students (4 females, 3 males) with normal or corrected-to-normal vision 94 participated in the experiment. Each of the subjects completed at least five experimental sessions with a 95 minimum of 300 valid decision trials each.

96

97 Experimental Setup

- 98 The subjects sat in front of a 22" flat-screen CRT video monitor (ViewSonic P225f; viewing distance:
- 99 60 cm) with their head on a chin and forehead rest. The visual stimuli were generated by a Macintosh
- 100 G4 computer running Mac OS 9, MATLAB (The Mathworks, Natick, MA), and the Psychophysics Toolbox
- 101 (Brainard, 1997; Pelli, 1997) at a frame rate of 75 Hz. The experiment was controlled and the data were
- 102 collected by an Intel Pentium IV computer running QNX (Ottawa, ON, Canada) and a modified version of
- 103 REX (Laboratory of Sensorimotor Research, National Eye Institute).
- 104 Eye movements were monitored using a monocular IR video eye tracker with chinrest-mounted optics
- 105 (Series 5000, Applied Science Laboratories, Bedford, MA) operating at 240 Hz. Prior to each
- 106 experimental session the eye tracker was calibrated using repeated fixation of nine calibration targets
- 107 with horizontal eccentricities of -10, 0, and +10 deg and vertical eccentricities of -7.5, 0, and +7.5 deg.

108

110 Experimental Task and Visual Stimulus

111 The experimental task is illustrated in Fig. 1. Each trial started with the presentation of a central fixation 112 mark (diameter: 0.3 deg). The measured fixation location had to remain within 2.5 deg of the center of 113 the screen throughout the trial (up to the saccadic response). After 250 to 500 ms of stable fixation, 114 three targets (diameter: 0.5 deg) appeared on the screen, all located on a virtual circle around the 115 fixation mark with a radius of 8.0 deg. The target locations were chosen randomly (with equal spacing) 116 at the beginning of an experimental sessions and did not change throughout the session. After another 117 random delay of 250 to 500 ms, a multi-component random-dot pattern was presented at the center of 118 the screen (diameter: 5.0 deg).

119 In the original version of the stimulus (as used, e.g., in Shadlen and Newsome, 2001; Roitman 120 and Shadlen, 2002; Palmer et al., 2005) a certain fraction of the dots (defined as the coherence of the 121 stimulus) was moving coherently in a particular direction, whereas the remaining dots were flickering 122 randomly. Our multi-component random-dot pattern had up to three coherent motion components 123 embedded. Thus, there were four subpopulations of dots: one was moving coherently in a particular 124 direction θ (aligned with one of the choice targets; fraction of dots defined by the coherence of the first 125 component), another one was moving coherently in the direction $\theta + 120^{\circ}$ (fraction defined by the 126 coherence of the second component), a third one was moving coherently in the direction $\theta + 240^{\circ}$ 127 (fraction defined by the coherence of the third component), and the remaining dots were flickering 128 randomly. The stimulus is therefore described by a set of three coherences. Which of the four 129 subpopulations a particular dot belonged to, changed randomly over time. As a consequence, the 130 stimulus is not perceived as an overlay of several transparent layers of motion that could be easily 131 separated, but as a mixture of different motion components. See, e.g., Treue et al. (2000) for a 132 discussion of transparent random-dot motion stimuli. Corresponding pairs of dots, responsible for the

percept of apparent motion, were presented with a temporal separation of 40 ms (3 video frames). The coherently moving dots had a speed of 6 deg/s, the dot density was $16.7 \frac{dots}{deg^2 \cdot s}$, and each dot was a little filled square with an edge length of 0.1 deg. On each trial, the set of coherences was randomly selected from a list of 51 possible coherence combinations ranging from 0 to 40% each. The full list can

137 be found in Table 1.

138

139 The subjects were instructed to identify the direction of the strongest motion component and to make a 140 saccadic eye movement to the associated choice target (aligned with the identified direction of motion). 141 They were allowed to watch the stimulus for as long as they wanted (up to 5 s) and to respond 142 whenever they were ready. The motion stimulus disappeared from the screen as soon as the eye left the 143 central fixation window. Subjects were further instructed to indicate with a second saccadic eye 144 movement to one of the two remaining choice targets, which of the remaining options they would 145 rather bet on as a second guess, assuming they got their first choice wrong. After each trial they 146 received auditory feedback as to whether they had picked the correct target in their primary choice. In 147 case the stimulus did not have one strongest motion component, the computer randomly identified one 148 of the targets as being the correct one. No feedback was given on the second guess.

In order to complete a trial successfully ("valid trial"), the subject had to maintain accurate fixation until the random-dot pattern appeared. Once central fixation was broken, the eye position had to be within 3 deg of one of the three choice targets within 100 ms and had to stay on this target (primary choice) for at least 200 ms. At this point, a neutral sound was played, indicating that the primary choice had been registered, but not providing any information about its accuracy yet. At most 3 s later, the eye position had to be within 3 deg of one of the remaining choice targets and had to stay on this target (second

guess) for at least 200 ms. At this point, auditory feedback was given about the accuracy of the primarychoice, which indicated to the subject that the trial had been registered as a valid trial.

157

158 Data Analysis

For analyzing the data, we collapsed across different target locations. Thus, we only worked with the 15 unique sets of coherences (eliminating the permutations) and whether the subject picked the target associated with the strongest motion component, the one associated with the intermediate component, or the one associated with the weakest component. We analyzed the pooled data across subjects to have a robust number of trials for each experimental condition. Since we only work with mean RTs in this study, we were not concerned about variability in RT across subjects potentially affecting the shape

- 165 of RT distributions.
- 166 RT was defined as the time between the appearance of the random-dot stimulus and the breaking of
- 167 central fixation. We did not analyze the timing of the second guess as subjects had to wait for their
- 168 primary choice to be registered by the computer before they could report their second guess. Thus, the

timing of the second guess was largely externally imposed.

170

171 <u>Computational Models</u>

172 Model of the neural representation of the sensory stimulus

- 173 The mean response of a population of motion-sensitive neurons to a 3-component random-dot stimulus
- 174 with coherences c_1 (in the preferred direction of the pool), c_2 , and c_3 was modeled to be of the form

175
$$\overline{s_1} = \frac{g \cdot \left[c_1 + k_n \cdot \left(1 - \sum_{i=1}^3 c_i\right)\right]}{1 + k_s \cdot (c_2 + c_3)}$$

176 where g is the overall gain of the sensory response (relationship between neural activity and motion 177 strength). The two additive terms in the brackets reflect the two linear response components: the first describes the response to the coherent motion in the preferred direction, the second describes the 178 179 response to the noise dots. The term in parenthesis reflects the proportion of noise dots in the stimulus. k_n is the relative gain of the response to the noise dots compared to the response to an identical 180 fraction of dots moving coherently in the preferred direction. The term in the denominator reflects the 181 182 divisive normalization. Since the term in the numerator accurately describes the response to a single-183 component stimulus, only the coherences of motion components with directions other than the 184 preferred one are present in the denominator. For simplicity, we have chosen a linear term, with $k_{\rm c}$ 185 describing the gain/strength of the divisive normalization (Niwa and Ditterich, 2008).

186 In general, the mean responses of each of the three task-relevant sensory pools can be written as

187
$$\overline{s_j} = \frac{g \cdot \left[c_j + k_n \cdot \left(1 - \sum_{i=1}^3 c_i\right)\right]}{1 + k_s \cdot \sum_{i \neq j} c_i}$$

188 The variances of the three sensory responses were modeled as

189
$$\sigma_{s_j}^2 = k_v \cdot \overline{s_j}$$

We described the outputs of the sensory pools as normal random processes to be able to treat the
 decision process as a standard diffusion process (based on Brownian motion), which is reasonable if the
 pools are not too small.

194 Model of the decision process

In principle, we would have to treat the race between the three integrators mathematically as a 195 196 3-dimensional diffusion process. However, for the 2AFC case, the decision process has often been 197 described as a 1-dimensional diffusion process with two boundaries instead of a 2-dimensional diffusion 198 process. This simplification can be done when one assumes that the two signals that are accumulated by 199 the two integrators are only different in sign, but identical in absolute value. Such a situation would 200 result from all of the contributions that a particular pool of sensory neurons makes to the net evidence 201 signals having the same origin. If we make the same assumption in our model, we can also reduce the 202 dimensionality of the problem. We can write the three evidence signals as

203

$$e_{1} = s_{1} - \frac{1}{2}s_{2} - \frac{1}{2}s_{3}$$
$$e_{2} = s_{2} - \frac{1}{2}s_{1} - \frac{1}{2}s_{3}$$
$$e_{3} = s_{3} - \frac{1}{2}s_{1} - \frac{1}{2}s_{2}$$

204 e_3 can be rewritten as

205
$$e_3 = -(s_1 - \frac{1}{2}s_2 - \frac{1}{2}s_3) - (s_2 - \frac{1}{2}s_1 - \frac{1}{2}s_3) = -e_1 - e_2$$

Thus, if e_1 and e_2 are known, e_3 is known. In our model, each of the three evidence signals is integrated over time (see Fig. 2):

208
$$i_j(t) = \int_0^t e_j(\tau) d\tau$$

Since integration is a linear operation, if i_1 and i_2 are known, i_3 is also known. We can therefore rewrite the decision criterion for choosing the 3rd alternative:

$$\begin{array}{rcl}
i_3 &> 1\\ -i_1 - i_2 &> 1\\ i_2 &< -i_1 - 1\end{array}$$

Thus, the third integrator exceeding a value of 1 is equivalent to crossing another linear boundary in the $i_1 - i_2$ plane (for an illustration see Niwa and Ditterich (2008), Fig. 3C). The diffusion process always starts at (0;0) and stops when one of the three boundaries is crossed: $i_1 = 1$ is the decision boundary for the 1st alternative, $i_2 = 1$ is the boundary for the 2nd alternative, and $i_2 = -i_1 - 1$ is the boundary for the 3rd alternative.

217 The 2-dimensional diffusion process is described by a drift vector and a covariance matrix. The drift

218 vector is given by
$$\begin{bmatrix} \overline{e_1} \\ \overline{e_2} \end{bmatrix}$$
, the means of the first two evidence signals. Since $\begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$ can be calculated as

219
$$\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} 1 & -\frac{1}{2} & -\frac{1}{2} \\ -\frac{1}{2} & 1 & -\frac{1}{2} \end{bmatrix} \cdot \begin{bmatrix} s_1 \\ s_2 \\ s_3 \end{bmatrix}$$

220
$$\left[\frac{\overline{e_1}}{\overline{e_2}}\right]$$
 is given by

221
$$\begin{bmatrix} \overline{e_1} \\ \overline{e_2} \end{bmatrix} = \begin{bmatrix} 1 & -\frac{1}{2} & -\frac{1}{2} \\ -\frac{1}{2} & 1 & -\frac{1}{2} \end{bmatrix} \cdot \begin{bmatrix} \overline{s_1} \\ \overline{s_2} \\ \overline{s_3} \end{bmatrix}$$

222 The covariance matrix Σ can be calculated as

$$\begin{split} \Sigma = & \begin{bmatrix} 1 & -\frac{1}{2} & -\frac{1}{2} \\ -\frac{1}{2} & 1 & -\frac{1}{2} \end{bmatrix} \cdot \begin{bmatrix} \sigma_{s_1}^2 & 0 & 0 \\ 0 & \sigma_{s_2}^2 & 0 \\ 0 & 0 & \sigma_{s_3}^2 \end{bmatrix} \cdot \begin{bmatrix} 1 & -\frac{1}{2} \\ -\frac{1}{2} & 1 \\ -\frac{1}{2} & -\frac{1}{2} \end{bmatrix} = \\ = & \begin{bmatrix} \sigma_{s_1}^2 + \frac{1}{4}\sigma_{s_2}^2 + \frac{1}{4}\sigma_{s_3}^2 & -\frac{1}{2}\sigma_{s_1}^2 - \frac{1}{2}\sigma_{s_2}^2 + \frac{1}{4}\sigma_{s_3}^2 \\ -\frac{1}{2}\sigma_{s_1}^2 - \frac{1}{2}\sigma_{s_2}^2 + \frac{1}{4}\sigma_{s_3}^2 & \frac{1}{4}\sigma_{s_1}^2 + \sigma_{s_2}^2 + \frac{1}{4}\sigma_{s_3}^2 \end{bmatrix} = \\ = & k_v \cdot \begin{bmatrix} \overline{s_1} + \frac{1}{4}\overline{s_2} + \frac{1}{4}\overline{s_3} & -\frac{1}{2}\overline{s_1} - \frac{1}{2}\overline{s_2} + \frac{1}{4}\overline{s_3} \\ -\frac{1}{2}\overline{s_1} - \frac{1}{2}\overline{s_2} + \frac{1}{4}\overline{s_3} & \frac{1}{4}\overline{s_1} + \overline{s_2} + \frac{1}{4}\overline{s_3} \end{bmatrix} \end{split}$$

225 Model of the second choice based on accumulated evidence at or shortly after the time of the first
226 threshold crossing

227 The integrator crossing the decision threshold first determines the primary choice and the decision time. 228 We propose that the state of the remaining integrators at the time when the winning integrator crosses 229 threshold can be used to determine the second guess. The higher value of the two remaining integrators 230 determines the second choice. For example, if the second integrator crossed the threshold first, the 231 states of the first and the third integrator at this particular time would be compared, and the larger 232 value would determine the second guess. As pointed out above, when working with a 2-dimensional 233 stochastic process, the two dimensions correspond to the states of the first two integrators. The state of the third integrator can be calculated as $i_3 = -i_1 - i_2$. 234

235 While the first passage time problem could be solved numerically (see Ditterich, 2006, section B.5 and

- Niwa and Ditterich, 2008), we also needed the predictions for the distribution of second choices.
- 237 Therefore, we discretized the 2-dimensional diffusion process (time step: 5 ms) and simulated 50,000
- trials per experimental condition. The MATLAB function OU_2D_3B_SIM_SC.M, which has been used for
- 239 performing the model calculations, is part of the Stochastic Integration Modeling Toolbox (SIMT; written
- 240 by JD), which can be downloaded from https://www.github.com/peractionlab/StochInt.

To determine whether the second guess might have been informed by sensory evidence that arrived at the decision process after the decision threshold had been crossed, we allowed the integration process to continue for a fixed amount of time after the threshold crossing and then read out and compared the states of the integrators that had not won the race to threshold. The MATLAB function used for this purpose, OU_2D_3B_SIM_SC_ADD_TIME.M, is also part of SIMT. To quantify the deviation between predicted and observed second guesses, we calculated the sum of the squared differences between predicted and observed relative frequencies.

248

249 Model of the second choice based on two successive threshold crossings

We also considered a model where the integration process continues after the first threshold crossing, until a second (different) bound is crossed. The first threshold crossing determines the first choice, the second threshold crossing the second choice and the decision time. In contrast to our original model, to give this model more flexibility, the integration of sensory evidence was allowed to be leaky (the time constant of integration was an additional free model parameter), and the bounds were allowed to collapse over time. We used the same logistic function as in Ditterich (2006):

256
$$A(t) = \frac{1}{1 + \exp(s \cdot (t - d))} + \frac{\exp(-s \cdot d)}{1 + \exp(-s \cdot d)}$$

t is the time into the decision process, and s and d are two additional free model parameters that
define the shape (slope) and the position (delay) of the collapsing bound. The MATLAB function
OU_2D_3B_TWO_CROSS_SIM.M, which was used for evaluating this model, is also part of SIMT.

260

262 Models of the second choice based on two successive decision processes

Another class of models involved starting a new decision process when the first threshold crossing occurred, but only between the two alternatives that did not win the original race to threshold. For example, assuming that i_2 crossed the threshold first, the second process would be set up as

$$e'_1 = s_1 - s_3$$

 $e'_2 = s_3 - s_1$

267 If the integral of the first evidence signal crossed the threshold first, Direction 1 would be reported as 268 the second choice. If the integral of the second evidence signal crossed the threshold first, Direction 3 would be reported as the second choice. Since $e'_2 = -e'_1$, this second decision process can be treated as 269 270 a 1-dimensional drift-diffusion process with two boundaries. The decision time would be the total 271 duration of both decision processes. To give this model more flexibility, we allowed the decision 272 threshold of the second decision process to be lower than the decision threshold of the first decision 273 process. The second decision threshold was an additional free model parameter. The MATLAB function 274 OU_2D_3B_1D_2B_SIM_SC.M, which has been used for evaluating this model, is also part of SIMT. 275 Finally, we considered a model that also starts a second decision process when the first threshold 276 crossing occurs, but it does not wait for a second threshold crossing. The second decision process 277 unfolds for a fixed amount of time and is then read out. The sign of the current state of the integrated 278 evidence (of the 1D process) determines the second choice. The MATLAB function 279 OU_2D_3B_1D_FIXED_TIME_SIM_SC.M, which was used for evaluating this model, is also part of SIMT.

280

282 Model Fit

283 The model parameters were identified by an optimization procedure based on the mean RTs. A 284 combination of a global pattern search (provided by MATLAB's Global Optimization Toolbox) and a 285 multi-dimensional simplex algorithm (provided by MATLAB's Optimization Toolbox) was used to 286 minimize the sum of the squared differences between the mean RTs in the data and the mean RTs 287 predicted by the model, taking the standard errors of the estimated means into account. We used the 288 mean RTs for each combination of coherences, regardless of choice (15 data points). For the model 289 these were obtained by calculating a weighted sum of the predicted mean RTs for the different choices 290 based on the predicted probabilities of these choices.

291

292 RESULTS

- 293 We used 11,060 valid decision trials from seven subjects for analysis and modeling. The overall accuracy
- of the primary choice was 72% (chance level would be 33% for a 3AFC task), which provided us with
- 295 7,951 correct trials and 3,109 error trials for further analysis. How the primary choice and the associated
- 296 RT depended on the presented stimulus was similar to what we had reported in Niwa and
- 297 Ditterich (2008) and will be presented in the context of a computational model below.

298

299 Second guesses in perceptual decision-making are informed by sensory evidence

300 To test whether subjects are able to make an informed second guess, we analyzed the error trials and

- 301 quantified how often subjects reported what would have been the correct choice as their second guess.
- 302 If subjects just guessed randomly, this should not deviate significantly from chance (50%). The correct
- 303 option, however, was reported as the second guess in 63% of the error trials, which is highly significantly

above chance ($p < 10^{-6}$; binomial test). This indicates that the second guess was clearly informed by the sensory evidence provided by the motion stimulus.

306

307 A computational model that can explain primary choices and associated RTs

308 To gain more insight into what information the second guesses were based on, we resorted to 309 computational modeling. In Niwa and Ditterich (2008) we presented an integration-to-threshold model 310 that was able to explain the distribution of choices in the 3-choice multi-component RDM direction 311 discrimination task as well as the associated RTs. Briefly, in a stochastic process, we modeled three pools 312 of motion-sensitive neurons (for each of the possible directions). Each of these pools had a strong linear 313 response to coherent motion in its preferred direction, a weak linear response to the randomly moving 314 dots in the stimulus, and divisive normalization based on how much coherent motion the stimulus 315 contained driving the other pools. The variance of each pool's output scaled linearly with its mean. The 316 net sensory evidence for each direction, calculated as the difference between one pool's activity and the 317 average activity of the other two, was then fed into an integrator, one for each possible choice. 318 Whichever integrator reached a constant decision threshold first determined the choice, and the time of 319 crossing the decision threshold the decision time. RT was modeled as the sum of the decision time and a 320 fixed residual time, capturing the time needed for aspects of the task other than the decision itself, e.g., 321 initiating an eye movement for reporting the choice. The structure of the model is shown in Figure 2. 322 Further details can be found in Materials and Methods. 323 If adding the secondary task of reporting a second guess did not alter the way subjects made their 324 primary choice, the same model should still be able to capture the primary choice data and associated 325 RTs from this experiment. To test this, we fitted the model (5 free parameters) to the mean RT data. The 326 result of this fit is shown in Figure 3. Filled circles represent the data (with 95% confidence intervals,

calculated according to the method proposed by Goodman, 1965), lines the model. The motion strength
of the strongest motion component in the stimulus is plotted on the horizontal axis, the color of
symbols/lines reflects the strength of the other two motion components. The model clearly captures the
structure of the mean RT data. If the model were perfect, at least 95% of the evaluated model mean RTs
would be expected to be within the 95% confidence intervals associated with the data. Our model is
close to that: 13 of the 15 mean RTs (87%) are inside, the two that are outside are still close to the
confidence intervals. The estimated model parameters are summarized in Table 2.

334 To further test whether the model can explain the primary choice data, we compared the model's 335 prediction for the distribution of primary choices with the actual distribution from the experiment 336 (Figure 4). These data have not been used yet, because the model had only been fitted to mean RT data. 337 The plotting conventions are similar to Figure 3. Circles indicate correct choices, squares choices of the 338 direction that had intermediate support, and diamonds choices of the direction that had the weakest 339 support. A perfect model would predict probabilities, at least 95% of which would be expected to be 340 within the 95% confidence intervals associated with the data. While our model is not perfect, 18 of the 341 23 probabilities (78%) are inside, the five that are outside are still close to the confidence intervals. The 342 good agreement between data and model predictions indicates that the model introduced in Niwa and 343 Ditterich (2008) is still able to explain the primary choice data and associated RTs from the current 344 experiment. Thus, asking subjects to report a second guess apparently did not alter the structure of the 345 decision process.

346

347 The same computational model can also explain second guesses

We have demonstrated earlier that subjects can produce informed second guesses when making
perceptual decisions between multiple alternatives, but can we gain insight into what governs these

350 second guesses? The idea behind the highly successful integration-to-threshold models in perceptual 351 decision-making is that decisionmakers accumulate sensory evidence for each of the possible choices 352 until the accumulated evidence for one of them exceeds a decision threshold. How could a subject make 353 an informed second guess in this framework? Assume the decisionmaker had access to the states of the 354 integrators that did not win the race at the time of the threshold-crossing. What should the distribution 355 of second guesses look like if subjects reported the integrator with the overall second-highest 356 accumulated evidence as their second guess, or, equivalently, the option with the larger accumulated 357 evidence out of the two remaining ones? We took the model, which had been fitted to the mean RTs 358 associated with the primary choice and was able to explain the distribution of primary choices, and 359 obtained the expected distributions of second guesses based on the overall second-highest accumulated 360 evidence.

361 A comparison between the predicted distributions of second guesses and the actual data on correct 362 trials is shown in Figure 5. Symbols again represent the data (and 95% confidence intervals), lines reflect 363 the model predictions. On correct trials, by definition, subjects have already reported the correct option 364 as their primary choice. The correct option is therefore no longer available as a second guess. The 365 relative frequency of reporting the correct option as the second guess (filled circles) has to be zero. The 366 only interesting cases are those where the two weaker motion components had different motion 367 strengths (purple and cyan). Squares indicate how often subjects reported the direction with the 368 intermediate motion strength as their second guess, diamonds how often the weakest motion 369 component was reported.

The same comparison, but now for error trials, is shown in Figure 6. In this case, the correct option can be reported as the second guess, and we had already seen earlier that, across experimental conditions, it was chosen more frequently than chance. The figure shows this relative frequency broken down by experimental condition (circles), adds the relative frequencies of reporting each incorrect option as the

374 second guess (squares and diamonds), and provides the model predictions for comparison. Why, in 375 contrast to the plots we had seen so far, are the squares below the diamonds in this figure? When 376 reporting their primary choice, subjects were more likely to make an error in favor of the motion 377 component with intermediate support rather than picking the weakest component (see squares and 378 diamonds in Figure 4). The weakest component (diamonds) was therefore available as an option for the 379 second guess in substantially more error trials than the component with the intermediate support 380 (squares), which explains why it was overall chosen more frequently. And why does the probability of 381 reporting the direction of the strongest motion component (blue circles/line) not keep increasing 382 monotonically as a function of motion strength? To make an error in a trial with only a single motion 383 component with 40% coherence in the first place, the accumulated evidence for this direction has to be 384 unusually low. As a consequence, since the second guess is based on the same accumulated evidence, 385 there is also not a sufficient amount of evidence to support choosing this direction as the second guess. 386 A perfect model would again predict probabilities, at least 95% of which would be expected to be within 387 the 95% confidence intervals associated with the data. Across both correct and error trials and not 388 counting the zero-probability events, 26 of the 31 predicted probabilities (84%) are inside, the five that 389 are outside are still pretty close to the confidence intervals. Thus, there is good agreement between the 390 data and model predictions, indicating that the reported second guesses are consistent with the idea 391 that the decisionmaker has access to information about how much sensory evidence had been 392 accumulated for competing unchosen options at the time when sufficient evidence had been collected 393 to commit to a primary choice.

In summary, a computational model with only five free parameters can account for 15 mean RTs, 16
relative frequencies for the primary choice (not counting the 7 trivial cases of uniform choice
distributions when all motion components are equally strong and the relative frequency of choosing the
third option having to be one minus the sum of the relative frequencies of choosing the first or the

second option), and 18 relative frequencies for the second guess, again excluding the trivial cases. This
strongly suggests that the primary choice and the second guess are produced by a common integrationto-threshold decision process.

401

402 Second guesses are best explained by the states of the integrators shortly after threshold crossing 403 While the motion stimulus disappeared from the screen when the saccade for reporting the primary 404 choice was detected, there is a delay between the decision threshold crossing and the saccade onset, 405 and some stimulus information is also still in the visual cortical processing pipeline. In the decision 406 confidence literature, it has been proposed that the decision confidence, which is usually reported after 407 the choice, could be informed by sensory evidence that is processed after the choice has been made 408 (Pleskac and Busemeyer, 2010; Moran et al., 2015). To determine whether additional sensory evidence 409 might have contributed to the reported second guesses in our experiment, we created a variant of the 410 model, where the evidence accumulation was allowed to continue for a fixed period of time after the 411 decision threshold had been crossed, before the non-winning integrators were read out to determine 412 the second choice. Figure 7A shows the deviation between predicted and observed second guesses as a 413 function of the additional integration time. Since the calculated points (blue circles) are simulation-414 based and therefore slightly noisy, we added a robust polynomial interpolation (solid black line). The 415 best match between predicted and observed second guesses (discrepancy of 0.027) is obtained for an 416 additional integration time of 40 ms (dashed vertical line), i.e., when the integrators are read out shortly 417 after the threshold crossing. The discrepancy clearly increases for longer additional integration times. Thus, the second guesses seem to be affected by a small amount of sensory evidence that is processed 418 419 after the primary choice has been determined, but still largely rely on the same information, as typical 420 decision times in our experiment are an order of magnitude larger. The predicted relative frequencies of

second guesses for a model with 40 ms of additional integration time are shown in Figures 7B and C.
There is no major qualitative difference between these plots and Figures 5 and 6, the match between
model predictions (lines) and data (symbols) is just slightly better.

424

425 A model waiting for the same decision process to cross a second threshold can be ruled out

426 To determine whether the second guesses could also be explained by alternative mechanisms that do 427 not require reading out and comparing the accumulated evidence for the options that did not win the 428 race to threshold, we considered several alternative models. First, we evaluated the possibility that the decision process could continue after the first threshold crossing until a second (different) threshold is 429 430 crossed. The first threshold crossing would determine the primary choice, the second threshold crossing 431 the second choice and the decision time. One can imagine that in situations where there is much 432 stronger evidence for one particular choice compared to the other alternatives, such a second threshold 433 crossing is unlikely to occur within a reasonable amount of time, in particular when the integration is 434 perfect, and the decision bounds are fixed. We therefore also considered mechanisms with leaky 435 integration and collapsing decision bounds (Ditterich, 2006). It turns out, however, that this class of 436 models, even in the presence of leaky integration and collapsing bounds, makes one key qualitative 437 prediction: decision times should increase, rather than decrease, when the evidence gets stronger. As a 438 consequence, the best mean RT fit that can be obtained is largely flat as a function of motion strength, 439 and the remaining error is about 6 times as large as the one for the fit shown in Fig. 3. Figure 8A shows 440 this fitting attempt. This class of models can therefore be ruled out as an alternative explanation.

441

442

A model based on a second integration-to-threshold process for determining the second choice makes
less accurate predictions for the distribution of second quesses

445 We also considered the possibility that, as soon as the first threshold crossing occurs, a new decision 446 process, only as a 2AFC between the two remaining options, is started. A threshold crossing of the 447 second decision process would then determine the second choice and the decision time. When 448 enforcing the same decision threshold as in the primary decision process, the remaining error after the 449 mean RT fit is more than an order of magnitude larger than the one for the fit shown in Fig. 3. We 450 therefore considered the possibility that the decision threshold for the second decision process could be 451 lower. The mean RT fit reveals that the threshold would have to be very close to zero to be able to 452 account for the pattern of RTs. A fit with a decision threshold of 0.052 (compared to 1 in the case of the 453 first decision process) resulted in a remaining error that was only slightly larger than the one for the fit 454 shown in Fig. 3. We therefore determined the predicted second guesses for this model (shown in 455 Figure 8B and C). The discrepancy between predicted and observed second guesses, following the same 456 convention as the one used in Fig. 7A, was 0.129 (red dashed line in Fig. 8D), about five times as big as the one for the model shown in Fig. 7B and C. Thus, this model also cannot capture the data pattern as 457 458 well as our original model.

459

460 A model based on a second, fixed-duration decision process for determining the second choice provides
461 the second-best explanation for the distribution of second guesses

As a final possibility, we considered that the second decision process might not be terminated by a threshold crossing, but rather end after a fixed amount of time. The process would be read out at that point, and the sign of the accumulated evidence would determine the second choice. The discrepancy between predicted and observed second guesses for this model, as a function of the duration of the

466 second decision process, is shown in Figure 8D. Since the calculated points (blue circles) are simulation-467 based and therefore slightly noisy, we again added a robust polynomial interpolation (solid blue line). 468 The best match is observed for an integration time of 70 ms, but the discrepancy is still 0.081, about 469 three times as big as the one for the model shown in Fig. 7B and C (solid black in Fig. 8D). This model's 470 predictions for the second guesses are shown in Figures 8E and F. In contrast to our original model, 471 which predicted the nonmonotonic relationship between motion strength and the probability of 472 choosing the strongest motion component as the second guess on error trials (blue circles in Fig. 8F), 473 this model predicts a monotonic relationship (blue line). This difference results from the fresh start of 474 evidence accumulation in the second decision process, rather than the second guess being substantially 475 affected by the accumulated evidence that led to the primary choice. Since 70 ms are needed for the 476 second integration process, the residual time would be reduced to 593 ms in this case. While this model 477 provides the second-best explanation, our original model still provides the better explanation for the 478 observed pattern of second guesses.

479

480 **DISCUSSION**

481 We asked human subjects to make a perceptual decision among three alternatives and to report not 482 only their primary choice, but also a second guess. Our data indicate that this second guess is not 483 random, but clearly informed by the sensory evidence. A single integration-to-threshold model can not 484 only explain the distribution of primary choices and the associated RTs, but also the distribution of 485 second guesses. This suggests that the second guess is generated based on largely the same 486 accumulated evidence that is also used to produce the primary choice. The second guess appears to be 487 governed by the ranking of the amounts of evidence that have been accumulated by the integrators that 488 did not win the race to threshold, which are apparently accessible.

We also considered alternative models. The only other model that was able to largely capture the data pattern, although not as well as the model based on reading out the states of the integrators that had not crossed the decision threshold yet shortly after the winning integrator crossing its threshold, was a model based on starting a new decision process when the threshold crossing determining the primary choice occurred. The process had to be set up as a decision between the remaining alternatives and read out after a fixed amount of time (about 70 ms).

495

496 *Relationship with decision confidence*

497 Human subjects can not only report their choice when making a perceptual decision, but also express a 498 level of confidence in their decision. A substantial body of literature has been devoted to how well 499 calibrated this decision confidence is and how it might be computed. Ideally, the level of confidence 500 should match the accuracy of the decision. However, this is typically not the case, and human subjects 501 have been reported to be either under- or overconfident, depending on the difficulty of the decision 502 (see Rahnev and Denison, 2018 for a review). Confidence clearly is informed by the available sensory 503 evidence, but how? Vickers (1979) suggested that it depends on the balance of evidence. The more 504 dissimilar the amounts of evidence in favor of the available options are at the time of making a decision, 505 the more confident the observer can be about the choice. This information can be extracted from the 506 decision process itself. While the idea is incompatible with the popular 1-dimensional drift-diffusion 507 model for 2-alternative forced choices, which is equivalent to a race between two accumulators that 508 receive perfectly anti-correlated instantaneous net evidence and, as a consequence, always has the 509 losing integrator in an identical state when the winning integrator exceeds the decision threshold, it can 510 be applied to alternative models. For example, Ditterich (2006) demonstrated that a model based on 511 partially anti-correlated accumulators provides a better account of decision-related activity in the

512 parietal association cortex of monkeys performing a perceptual decision task. Neurons coding for the 513 losing alternative do not show a stereotyped activity level when the neurons coding for the winning 514 alternative reach threshold. This information could be used to inform confidence. Moreno-Bote (2010) 515 formalized how confidence can be extracted from diffusion models with partially correlated integrators. 516 An alternative mechanism was proposed by Smith and Vickers (1988). According to their model, only 517 one of the integrators is updated at a particular time, the one receiving positive instantaneous net 518 sensory evidence, which also results in the losing accumulator being in different states when the 519 winning accumulator reaches threshold.

520 Gaining neurophysiological insights into the neural mechanism underlying decision confidence from 521 animal experiments is challenging, as animals cannot be asked directly to provide an explicit confidence 522 rating. However, animal tasks have been developed, which require the animal to produce a behavior 523 that should be informed by decision confidence (see Hanks and Summerfield, 2017 for a review). For 524 example, Kiani and Shadlen (2009) trained monkeys to make a perceptual decision between two 525 alternatives. In a random subset of trials, the researchers offered a third option, a sure bet resulting in a 526 smaller, but certain reward, whereas the animals could gain a larger reward if they engaged in a choice 527 and reported the correct option. The animals were more likely to choose the sure bet the weaker the 528 sensory evidence (motion coherence) was and the shorter they were allowed to watch the motion 529 stimulus. Importantly, decision-related neurons in parietal association cortex that have the signature of 530 carrying accumulated evidence showed either strong or weak activation when the animal engaged in a 531 choice, but intermediate activation when opting for the sure bet, suggesting that the information 532 encoded in these neurons does not only govern choice, but also inform confidence. The study further 533 suggested that decision confidence does not only depend on accumulated evidence, but also on elapsed 534 time, which was confirmed explicitly in a later human psychophysics experiment (Kiani et al., 2014) and 535 is also formalized in Moreno-Bote's (2010) model. Animal experiments on decision confidence have

received some criticism, primarily claiming that the tasks could potentially be solved without requiring
any meta-cognition, for example, by treating tasks with a sure bet as a multi-alternative decision task
(Insabato et al., 2016, 2017). However, Kepecs and Mainen (2012) pointed out that the same scrutiny
should then also be applied to human tasks.

540 The view that confidence is governed by the same information that determines the choice and, in 541 particular, by the balance of evidence has been challenged by experiments that found that confidence 542 primarily relies on response-congruent evidence (Zylberberg et al., 2012; Maniscalco et al., 2016). The 543 authors reported that, while choices in their experiments were governed by the balance of evidence, 544 confidence was primarily determined by the amount of evidence for the chosen option and largely 545 insensitive to the amount of evidence for the non-chosen alternative. Dual stage or second-order 546 models are also at odds with the idea that choice and confidence rely on the same information (Pleskac 547 and Busemeyer, 2010; Moran et al., 2015; Fleming and Daw, 2017). These models posit that confidence 548 ratings rely on a post-decision process that is informed by the outcome of the decision process, but not 549 exclusively.

550 Different studies have therefore found the information upon which choice and decision confidence are 551 based to overlap to varying degrees. We have addressed a similar question for the mechanism 552 underlying second guesses. Our results indicate that the distribution of second guesses is most 553 compatible with a decision mechanism that largely uses the same accumulated evidence for 554 determining both the primary and the second choice. We found the best match between model 555 predictions and data, when the decision process was allowed to continue for a very short period of time 556 (compared to typical decision times in our experiment), about 40 ms, after the threshold crossing 557 determining the primary choice, before the states of the remaining integrators are read out to 558 determine the second choice.

560 Second guessing in other cognitive functions

561 In 1961, Signal Detection Theory (SDT) was still in its infancy and competing with the prevailing "high 562 threshold" model of sensory perception, Swets and colleagues published a paper proposing that a 563 second-choice paradigm in multi-interval signal detection could help distinguishing between the 564 competing ideas (Swets et al., 1961). However, second-choice paradigms have not been pursued further 565 in the area of perceptual decision-making, in particular not since the field has turned to sequential sampling models to explain not only choices, but also decision times. Instead, Swets et al.'s proposal got 566 567 picked up in the memory literature, there typically referred to as a 4AFC-2R (four-alternative forced 568 choice with two responses) paradigm, as the field was also debating whether recognition memory was 569 best described by a threshold process or by a continuous memory strength process. Parks and 570 Yonelinas (2009) used a second-choice paradigm to gather experimental evidence beyond the Receiver 571 Operating Characteristic analysis that the field had relied on previously. Kellen and Klauer (2011) 572 followed up with a more detailed model-based analysis. Earlier, second guesses had already been used 573 to study mechanisms underlying the effect of misinformation on memory recall (Wright et al., 1996). 574 More recently, second guesses have also been used to study conflict detection mechanisms in reasoning 575 (Bago et al., 2019).

576

577 Second guesses as a tool for studying knowledge about the decision process

We have shown that human subjects can produce informed second guesses when making perceptual decisions between multiple alternatives and that these second choices follow a distribution that would be expected if they were governed by the relative amounts of accumulated net sensory evidence for each option at the time of the largest accumulated evidence reaching a bound. Second-choice

paradigms therefore cannot only be used in the context of SDT, as they have in the past, but also with accumulation-of-evidence frameworks. In addition to decision confidence, the study of second guesses provides another useful tool for gaining insight into the decision process and what information a decisionmaker has access to about the outcome of a decision, beyond the discrete choice. Similar to the neurophysiological work on decision confidence, we expect future studies to be able to establish a link between second guesses and underlying neural activity.

588

589 **REFERENCES**

- 590 Bago B, Raoelison M, De Neys W (2019) Second-guess: Testing the specificity of error detection in the
- 591 bat-and-ball problem. Acta Psychol (Amst) 193:214-228.
- 592 Bollimunta A, Totten D, Ditterich J (2012) Neural dynamics of choice: single-trial analysis of decision-

593 related activity in parietal cortex. J Neurosci 32:12684-12701.

594 Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10:433-436.

- 595 Ditterich J (2006) Stochastic models of decisions about motion direction: behavior and physiology.
- 596 Neural Netw 19:981-1012.
- 597 Ditterich J (2010) A Comparison between Mechanisms of Multi-Alternative Perceptual Decision Making:
- 598 Ability to Explain Human Behavior, Predictions for Neurophysiology, and Relationship with

599 Decision Theory. Front Neurosci 4:184.

- 600 Fleming SM, Daw ND (2017) Self-evaluation of decision-making: A general Bayesian framework for
- 601 metacognitive computation. Psychol Rev 124:91-114.
- 602 Forstmann BU, Ratcliff R, Wagenmakers EJ (2016) Sequential Sampling Models in Cognitive
- 603 Neuroscience: Advantages, Applications, and Extensions. Annu Rev Psychol 67:641-666.

- Goodman LA (1965) On Simultaneous Confidence Intervals for Multinomial Proportions. Technometrics
 7:247-254.
- Hanks TD, Summerfield C (2017) Perceptual Decision Making in Rodents, Monkeys, and Humans. Neuron
 93:15-31.
- Insabato A, Pannunzi M, Deco G (2016) Neural correlates of metacognition: A critical perspective on
 current tasks. Neurosci Biobehav Rev 71:167-175.
- 610 Insabato A, Pannunzi M, Deco G (2017) Multiple Choice Neurodynamical Model of the Uncertain Option
- 611 Task. PLoS Comput Biol 13:e1005250.
- 612 Kellen D, Klauer KC (2011) Evaluating models of recognition memory using first- and second-choice
- 613 responses. J Math Psychol 55:251-266.
- Kepecs A, Mainen ZF (2012) A computational framework for the study of confidence in humans and
 animals. Philos Trans R Soc Lond B Biol Sci 367:1322-1337.
- 616 Kiani R, Shadlen MN (2009) Representation of confidence associated with a decision by neurons in the
- 617 parietal cortex. Science 324:759-764.
- Kiani R, Corthell L, Shadlen MN (2014) Choice certainty is informed by both evidence and decision time.
- 619 Neuron 84:1329-1342.
- Latimer KW, Yates JL, Meister ML, Huk AC, Pillow JW (2015) Single-trial spike trains in parietal cortex
 reveal discrete steps during decision-making. Science 349:184-187.
- 622 Luce RD (1986) Response Times: Their Role in Inferring Elementary Mental Organization: Oxford
- 623 University Press.
- 624 Maniscalco B, Peters MA, Lau H (2016) Heuristic use of perceptual evidence leads to dissociation
- between performance and metacognitive sensitivity. Atten Percept Psychophys 78:923-937.
- 626 Moran R, Teodorescu AR, Usher M (2015) Post choice information integration as a causal determinant of
- 627 confidence: Novel data and a computational account. Cogn Psychol 78:99-147.

- 628 Moreno-Bote R (2010) Decision confidence and uncertainty in diffusion models with partially correlated
- 629 neuronal integrators. Neural Comput 22:1786-1811.
- Niwa M, Ditterich J (2008) Perceptual decisions between multiple directions of visual motion. J Neurosci
 28:4435-4445.
- Palmer J, Huk AC, Shadlen MN (2005) The effect of stimulus strength on the speed and accuracy of a
 perceptual decision. J Vis 5:376-404.
- Parks CM, Yonelinas AP (2009) Evidence for a memory threshold in second-choice recognition memory
 responses. Proc Natl Acad Sci U S A 106:11515-11519.
- 636 Pelli DG (1997) The VideoToolbox software for visual psychophysics: transforming numbers into movies.
- 637 Spat Vis 10:437-442.
- Pleskac TJ, Busemeyer JR (2010) Two-stage dynamic signal detection: a theory of choice, decision time,
- and confidence. Psychol Rev 117:864-901.
- 640 Rahnev D, Denison RN (2018) Suboptimality in Perceptual Decision Making. Behav Brain Sci:1-107.
- 641 Ratcliff R, Smith PL (2004) A comparison of sequential sampling models for two-choice reaction time.
- 642 Psychol Rev 111:333-367.
- Ratcliff R, McKoon G (2008) The diffusion decision model: theory and data for two-choice decision tasks.
- 644 Neural Comput 20:873-922.
- Roitman JD, Shadlen MN (2002) Response of neurons in the lateral intraparietal area during a combined
 visual discrimination reaction time task. J Neurosci 22:9475-9489.
- 647 Shadlen MN, Newsome WT (2001) Neural basis of a perceptual decision in the parietal cortex (area LIP)
- of the rhesus monkey. J Neurophysiol 86:1916-1936.
- Smith PL, Vickers D (1988) The Accumulator Model of 2-Choice Discrimination. J Math Psychol 32:135168.
- 651 Swets J, Tanner WP, Jr., Birdsall TG (1961) Decision processes in perception. Psychol Rev 68:301-340.

- Treue S, Hol K, Rauber HJ (2000) Seeing multiple directions of motion-physiology and psychophysics. Nat
- 653 Neurosci 3:270-276.
- 654 Vickers D (1979) Decision Processes in Visual Perception: Academic Press.
- 655 Wright DB, Varley S, Belton A (1996) Accurate second guesses in misinformation studies. Appl Cognitive
- 656 Psych 10:13-21.
- 57 Zylberberg A, Barttfeld P, Sigman M (2012) The construction of confidence in a perceptual decision.
- 658 Front Integr Neurosci 6:79.

Table 1. List of motion coherence combinations

Motion coherence of first	Motion coherence of second	Motion coherence of third
component [%]	component [%]	component [%]
0	0	0
5	0	0
0	5	0
0	0	5
10	0	0
0	10	0
0	0	10
20	0	0
0	20	0
0	0	20
40	0	0
0	40	0
0	0	40
10	10	10
20	10	10
10	20	10
10	10	20
30	10	10
10	30	10
10	10	30

20	15	5
20	5	15
15	20	5
5	20	15
15	5	20
5	15	20
30	15	5
30	5	15
15	30	5
5	30	15
15	5	30
5	15	30
20	20	20
30	20	20
20	30	20
20	20	30
40	20	20
20	40	20
20	20	40
30	25	15
30	15	25
25	30	15
15	30	25

25	15	30
15	25	30
40	25	15
40	15	25
25	40	15
15	40	25
25	15	40
15	25	40

663 Table 2. Best-fitting model parameters

Model parameters	Parameter values
g	0.0103
k_n	0.197
k_s	0.616
k_{v}	0.329
Residual time (ms)	663



Figure 1. Experimental paradigm. Human subjects were asked to determine the strongest motion direction in a random-dot pattern with multiple motion components. They were free to watch the stimulus as long as they wanted and responded with a goal-directed eye movement to one of three choice targets to indicate their primary choice. Choices and RTs were measured. After indicating their primary choice, subjects were instructed to make a second goal-directed eye movement to one of the remaining two targets to indicate a second guess.

Sensory information

Integrators



676

675

Figure 2. Computational model. Three integrators (each associated with one of the three alternatives) race against each other. The integrator output signal (i_1 , i_2 , or i_3) reaching a decision threshold first determines the primary choice and terminates the decision process. The integrator input signals (e_1 , e_2 , and e_3) are net evidence signals, which are linear combinations of the three relevant sensory signals (s_1 , s_2 , and s_3). Solid arrows indicate positive weights (excitatory connections), and dashed arrows indicate negative weights (inhibitory connections). The second guess is determined by the rank ordering of the remaining two integrators when the winning one reaches threshold.



686

687 Figure 3. Mean response time data and fitted model. The symbols represent the measured mean RTs for 688 all unique combinations of motion strengths. The motion strength of the strongest component is plotted 689 on the horizontal axis. Colors indicate the motion strengths of the two weaker motion components. (For 690 example, the cyan point at 40% motion strength indicates the mean RT for stimuli with the three motion 691 components having strengths of 40%, 25%, and 15%, respectively.) Some points have been shifted 692 slightly horizontally to reduce graphical overlap. For example, all points within the gray bar centered on 693 20% have a strength of the strongest motion component of exactly 20%. Error bars indicate 95% 694 confidence intervals. The lines connect the mean RTs from the computational model.



Figure 4. Comparison between the relative frequencies of primary choices and model predictions.
Symbols again reflect the data, with error bars indicating 95% confidence intervals. The lines connect
the relative frequencies predicted by the computational model. Circles indicate choices of the target
associated with the strongest motion component (correct primary choices), squares choosing the target
associated with the component with intermediate motion strength, and diamonds choosing the target
associated with the weakest motion component. Other conventions as in Fig. 3. The dashed line
indicates chance performance.











Figure 7. Predictions for second guesses when integration is allowed to continue after the threshold
crossing. A. Discrepancy between predicted and observed second guesses as a function of additional
integration time before the accumulated evidence is read out. A minimum (best match) is observed at
40 ms. B. Predicted second guesses on correct trials with 40 ms additional integration time (same format
as Fig. 5). C. Predicted second guesses on error trials with 40 ms additional integration time (same
format as Fig. 6).



Figure 8. Alternative models. A. Mean RT fit for a model that waits for a second threshold crossing, but
 allowing leaky integration and collapsing bounds (same format as Fig. 3). B. Predicted second guesses on
 correct trials for a model that starts a new 2AFC decision process to determine the second choice and

731 waits for a threshold crossing, but allowing a lower threshold than in the primary decision process (same 732 format as Fig. 5). C. Like B, but for error trials (same format as Fig. 6). D. Discrepancy between predicted 733 and observed second guesses as a function of integration time for a model that starts a new 2AFC 734 decision process to determine the second choice and reads the process out after a fixed amount of time 735 (blue). A minimum (best match) is observed at 70 ms. For comparison, the curve for the original model 736 (black) and the value for the model with a low threshold (red) are also shown. E. Predicted second 737 guesses on correct trials for a model that starts a new 2AFC decision process to determine the second 738 choice and integrates the sensory evidence for 70 ms before the process is read out (same format as 739 Fig. 5). **F.** Like E, but for error trials (same format as Fig. 6).