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# Autistic traits, but not schizotypy, predict increased weighting of sensory information in Bayesian visual integration

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#### 11 Abstract

12 Recent theories propose that schizophrenia/schizotypy and autistic spectrum disorder are 13 related to impairments in Bayesian inference i.e. how the brain integrates sensory information (likelihoods) with prior knowledge. However existing accounts fail to clarify: i) 14 how proposed theories differ in accounts of ASD vs. schizophrenia and ii) whether the 15 impairments result from weaker priors or enhanced likelihoods. Here, we directly address 16 these issues by characterizing how 91 healthy participants, scored for autistic and schizotypal 17 traits, implicitly learned and combined priors with sensory information. This was 18 accomplished through a visual statistical learning paradigm designed to quantitatively assess 19 variations in individuals' likelihoods and priors. The acquisition of the priors was found 20 to be intact along both traits spectra. However, autistic traits were associated with more 21 veridical perception and weaker influence of expectations. Bayesian modeling revealed that 22 this was due, not to weaker prior expectations, but to more precise sensory representations. 23

#### 25 Introduction

In recent years Bayesian inference has come to be regarded as a general principle of brain 26 27 function that underlies not only perception and motor execution, but hierarchically extends all the way to higher cognitive phenomena, such as belief formation and social cognition. 28 Impairments of Bayesian inference have been proposed to underlie deficits observed in mental 29 illness, particularly schizophrenia 1-3, 49-51 and autistic spectrum disorder (ASD) 4-7. The general 30 hypothesis for both disorders is that the weight, also called "precision", ascribed to sensory 31 evidence and prior expectations is imbalanced, resulting in sensory evidence having relatively 32 33 too much influence on perception.

In schizophrenia, overweighting of sensory information could explain the decreased
susceptibility to perceptual illusions<sup>8</sup>, as well as the peculiar tendency to jump to conclusions<sup>9</sup>.
Moreover, the systematically weakened low-level prior expectations might lead to forming
compensatory strong and idiosyncratic high-level priors (beliefs), which would explain the
emergence and persistence of delusions as well as reoccurring hallucinations<sup>1-3</sup>.

In ASD, the relatively stronger influence of sensory information could explain hypersensitivity 39 to sensory stimuli and extreme attention to details. The weaker influence of prior expectations 40 would also result in more variability in sensory experiences. The desire for sameness and rigid 41 behaviors could then be understood as an attempt to introduce more predictability in one's 42 environment<sup>4</sup>. Furthermore, this could lead to prior expectations which are too specific and 43 which do not generalize across situations<sup>5</sup>. While all theories agree that the relative influence of 44 prior expectations is weaker in ASD, the primary source of this imbalance is debated: does it arise 45 from increased sensory precision (i.e. sharper likelihood) or from reduced precision of prior 46 expectations? <sup>10-12</sup> (Fig. 1). Some authors argue for attenuated priors <sup>4, 11</sup>, while others argue for 47 increased sensory precision<sup>6, 7, 10, 13</sup> but conclusive experimental evidence is lacking. **48** 

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Figure 1. Alternative hypotheses for ASD impairments within the Bayesian inference 53 framework. In Bayesian terms, the percept can be described as a posterior distribution, 54 which is a combination of sensory information (likelihood) and prior expectations (prior). 55 Two contrasting hypotheses have been proposed to underlie behavioral differences in ASD: 56 enhanced sensory precision, i.e. smaller  $\sigma_{sens}$  (left) vs. attenuated priors, i.e. larger  $\sigma_{exp}$ 57 (right). Both hypotheses predict a reduced influence (bias) of the prior on the location of the 58 posterior distribution (posterior mean). However, these alternatives differ in their predictions 59 60 for perceptual variability, which is determined by the posterior width: the enhanced sensory precision hypothesis should lead to reduced variability while the attenuated prior hypothesis 61 62 should lead to increased variability. By measuring both bias and variability, our experimental paradigm can distinguish between these two hypotheses. 63

A number of studies have aimed at testing Bayesian theories, either in a clinical population, or
by studying individual differences in the general population <sup>14-17</sup> under the hypothesis of a
continuum between autistic/schizotypal traits and ASD/schizophrenia <sup>18-20</sup>.

Attenuated slow-speed priors were reported in a motion perception task in individuals with ASD traits <sup>14</sup>. Autistic children also showed attenuated central tendency prior in temporal interval reproduction<sup>21</sup>. Attenuated priors were also reported in perceptual tasks that incorporate probabilistic reasoning <sup>15, 22</sup>. However, the direction of gaze priors <sup>23</sup> and the lightfrom-above priors <sup>24</sup> were found to be intact. Autistic children also demonstrated intact ability to update their priors in a volatile environment in a decision-making task <sup>25</sup> but a follow-up study in ASD adults showed that they overestimate volatility in a changing environment <sup>26</sup>.

In schizophrenia/schizotypal traits, Teufel et al.<sup>16</sup> reported increased influence of prior
expectations when disambiguating two-tone images, while Schmack et al.<sup>27,28</sup> reported weakened
influence of stabilizing predictions when observing a bistable rotating sphere.

Overall, the existing findings are not only mixed, but also employ very different paradigms, which makes their direct comparison difficult. Further, a critical limitation of most studies (except for Karaminis et al.<sup>21</sup>) is the lack of formal computational models that can test whether behavioral differences originate from different priors or from different likelihoods. Moreover, to our knowledge, despite the similarity of the Bayesian theories proposed for ASD and schizophrenia, there is no previous work investigating both autistic and schizotypal traits within the same experimental paradigm so as to test their differences.

85 We here address these questions empirically in a context of visual motion perception. We used a previously developed statistical learning task<sup>29</sup> in which participants have to estimate the 86 direction of motion of coherently moving clouds of dots (Fig. 2). Chalk et al.<sup>29</sup> found that in this 87 task healthy participants rapidly and implicitly develop prior expectations for the most 88 frequently presented motion directions. This in turn alters their perception of motion on low 89 contrast trials resulting in attractive estimation biases towards the most frequent directions. In 90 addition, prior expectations lead to reduced estimation variability and reaction times, as well as 91 increased detection performance for the most frequently presented directions. 92 When no stimulus is presented, the acquired expectations sometimes lead to false alarms (hallucinations), 93 again, mostly in the most frequent directions. Importantly, such biases were well described 94 using a Bayesian model, where participants acquired a perceptual prior for the visual stimulus 95 that is combined with sensory information and influences their perception. As such, this 96 paradigm is well suited to quantitatively model variations in likelihoods and priors in 97 individuals with ASD or schizotypal traits. 98





101 Figure 2: The moving dots task. (a) Sequence of events on a single trial. First, a fixation point

102 is presented. Next, a field of coherently moving dots is presented along with an estimation 103 bar (extending from the fixation point) which participants are required to move to indicate 104 perceived motion direction. Lastly, in a two-alternative forced choice, participants are asked 105 to report whether they saw the dots during the estimation part (detection task). (b) The 106 probability of different motion directions being presented: directions at ±32° are presented 107 more often than other directions. Motion direction is plotted relative to a central reference 108 angle (at 0°), which was randomly set for each participant.

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#### 110 Results

Here, we investigated individual differences in statistical learning in relation to autistic and schizotypal traits in a sample of 91 healthy participants. 8 participants failed to perform the task satisfactorily and were excluded from the analysis (see *Methods*), leaving 83 participants in the study (41 women and 42 men, age range: 18-69; mean: 25.7).

#### 115 Task behavior at low contrast

116 First, we investigated whether participants acquired priors on the group level. We discarded the 117 first 170 trials as that is how long it took for the 2/1 and 4/1 staircases contrast levels to converge (Appendix 1–Figure 2) and for prior effects to become significant (Appendix 1–Figures 3, 4 118 119 and 5). We analyzed task performance at low contrast levels (converged 2/1 and 4/1 staircases contrast levels) where sensory uncertainty is high. Replicating findings of Chalk et al. (2010), we 120 121 found that on the group level people acquired priors that approximated the statistics of the task. Such priors were indicated by: attractive biases towards  $\pm 32^{\circ}$  (Fig. 3a), less variability in 122 estimations at  $\pm 32^{\circ}$  (Fig. 3b; standard deviation of estimations  $11.9\pm 0.30^{\circ}$  at  $\pm 32^{\circ}$  versus 123 13.84±2.38° over all other motion directions; signed rank test: p< 0.001), shorter estimation 124 reaction times at  $\pm 32^{\circ}$  as compared to all other motion directions (Fig. 3c; average reaction time 125 was  $201.87 \pm 2.47$  ms at  $\pm 32^{\circ}$  versus  $207.75 \pm 2.60$  ms over all other motion directions; signed rank 126 test: p < 0.001) and better detection at  $\pm 32^{\circ}$  as compared to all other motion directions (Fig. 3d; 127 detected 75.57  $\pm$  0.65% at  $\pm$ 32<sup>°</sup> versus 66.70  $\pm$  0.83% over all other motion directions; signed rank 128 test: p < 0.001). 129

#### 131 No-stimulus performance

Another indicator of acquired priors is the distribution of estimation responses on trials when no actual stimulus was presented. We found that participants sometimes still reported seeing dots (experienced hallucinations) but mostly so around  $\pm 32^{\circ}$  (**Fig. 3f**, solid line). To quantify the statistical significance of hallucinations around  $\pm 32^{\circ}$ , the space of possible motion directions was divided into 45 bins of 16° and the probability of estimation within 8° of  $\pm 32^{\circ}$  was multiplied by the total number of bins:

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$$p_{rel} = p(\theta_{est} = \pm 32(\pm 8)) \cdot N_{bins}$$
, (1)

where Nbins is the number of bins (45), each of size 16°. This probability ratio would be equal to 1 if participants were equally likely to estimate within 8° of  $\pm 32°$ , as they were to estimate within other bins. We found that the median of Prel was significantly greater than 1 (median(Prel) = 1.6, p<0.001, signed rank test). Furthermore, the estimation distribution when no dots where detected (**Fig. 3f**, dash-dot line) was found to be significantly flatter (median(Prel) = 0, p < 0.001, signed rank test comparing with the median of Prel for hallucinations), suggesting that the hallucinations were indeed of perceptual nature (rather than related to a response bias).



147 Figure 3: Average group performance on low-contrast trials (a-d) and on trials with no

stimulus (e). (a) Mean estimation bias, (b) standard deviation of estimations, (c) estimation 148 reaction time and (d) fraction of trials in which the stimulus was detected. (f) Probability 149 distribution of estimation responses on trials without stimulus. The solid line denotes the 150 estimation responses when participants reported detecting a stimulus (hallucinations). The 151 152 dash-dot line denotes estimation distributions when participants correctly reported not 153 detecting a stimulus. (e) Distribution of hallucinations for high and low AQ groups (median split). The vertical dashed lines correspond to the two most frequently presented motion 154 directions (±32°). Error bars and shaded areas represent within-subject standard error. 155

156 Figure 3 – source data 1

This zip archive contains .csv files with all of the data that was used to produce plots in Fig. 3. 157 EstimationBias.csv contains estimation biases at each of the 9 presented angles. 158 EstimationVariability.csv contains standard deviation of estimations at each of the 9 159 presented angles. NostimDetected.csv and NostimUndetected.csv contain estimation 160 161 responses when stimulus was detected and not detected, respectively, on no-stimulus trials. Traits.csv contains AQ scores of each individual (column 3) as well as all other traits. 162 SourceData Readme.txt contains more detailed description of each data file. The plots can be 163 reproduced from MATLAB script master.m which is available in the provided Source Code 164 File 1. SourceCode Readme.txt contains more detailed description of the source code. 165

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#### 171 Task performance and autistic/schizotypy traits

Participants were prescreened to make sure they covered a wide range of autistic and
schizotypy scores. The AQ scores in our sample ranged from 6 to 41 with a mean (±SD) of 20.3
(±8.3). The RISC scores ranged from 8 to 55 with a mean of 31.7 (±11.9), and the SPQ scores
ranged from 4 to 59 with a mean of 26.4 (±13.8).

We found that on low contrast trials autistic traits lead to less variability in estimations (**Fig. 4b**; mean standard deviation of estimations: r = -0.327, p < 0.001), which remained significant after Bonferroni correction (p = 0.002). Moreover, there was a negative relationship between autistic 179 traits and estimation bias, which was trending according to robust regression (Fig. 4a; mean absolute estimation bias: r = -0.175, p = 0.053) and significant according to Kendall's correlation 180  $(\tau_b = -0.163, p = 0.032)$ , however, it did not survive Bonferroni correction (p = 0.212). In the 181 Bayesian framework, less bias could arise either due to wider priors or narrower sensory 182 likelihoods, while less variability could be a result of either narrower priors or narrower 183 184 likelihoods (see Fig. 1). Thus, observing less bias and less variability together suggests that the effects are driven by narrower likelihoods. An alternative is that the differences in variability 185 could be due to differences in motor precision, which we further assess via modeling (below). 186



Figure 4: Correlations between AQ scores and task performance on low contrast trials (a, b) and when no stimulus is presented (c). (a) Mean absolute bias (r = -0.175, p = 0.053), (b) mean standard deviation (i.e. variability) of estimations (r = -0.327, p < 0.001), and (c) the total number of hallucinations (r = -0.238, p = 0.010). The blue lines are robust regression slopes.

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#### 193 Figure 4 – source data 1

This zip archive contains .csv files with all of the data that was used to produce plots in Fig. 4. 194 195 EstimationBias.csv contains estimation biases at each of the 9 presented angles. EstimationVariability.csv contains standard deviation of estimations at each of the 9 196 197 presented angles. NostimDetected.csv contains the number of hallucinations at different 198 directions. Traits.csv contains AQ scores of each individual (column 3) as well as all other traits. SourceData\_Readme.txt contains more detailed description of each data file. The plots 199 were produced with MATLAB script analyze data.m which is available in the provided 200 Source Code File 1. SourceCode\_Readme.txt contains more detailed description of the source 201 202 code.

Schizotypy traits (RISC and SPQ scores) did not show any effect on task performance at low contrast as indicated by the absence of correlations with mean absolute estimation bias (RISC: r =0.140, p = 0.197; SPQ (N=39): r = -0.160, p = 0.204) and with mean estimation variability (RISC: r =0.197, p = 0.092; SPQ (N=39): r = -0.229, p = 0.171); see **Appendix 1–Figures 6, 7 and 8**.

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#### 210 No-stimulus trials and autistic/schizotypal traits

211 We also investigated how the traits affected performance on trials when no actual stimulus was presented. First, we looked at the total number of estimations. We found that autistic traits were 212 213 associated with less hallucinations (Fig. 4c; r = -0.238, p = 0.010), while schizotypal traits were found 214 to have no effect on the number of hallucinations (RISC: r = 0.126, p = 0.163; SPQ (N=39): r = -0.010, p = 0.959). Secondly, we looked for relationships between the traits and how the estimations 215 on no-stimulus trials were distributed. Specifically, we were interested in whether the traits 216 predicted how densely hallucinations were distributed around  $\pm 32^{\circ}$ , as this could be considered 217 to reflect the differences in the width of the underlying acquired prior distribution. For weaker 218 219 priors we would expect a more spread out distribution of hallucinations. To test this hypothesis, we looked at the fraction of total hallucinations in the region around  $\pm 32^{\circ}$  for three different-220 sized windows: Within  $8^{\circ}$ , within  $16^{\circ}$  and within  $24^{\circ}$  of  $\pm 32^{\circ}$ . Bayesian Kendall correlation 221 analysis on these measures provided positive evidence that none of the traits had any effect on 222 how hallucinations were distributed, suggesting no differences in the acquired prior 223 distributions (fraction of hallucinations within  $8^{\circ}$  of  $\pm 32^{\circ}$ : AQ -  $\tau_b = 0.003$ , BF<sub>01</sub> = 7.24; RISC -  $\tau_b = -$ 224 0.050, BF<sub>01</sub> = 3.73; SPQ -  $\tau_b$  = 0.101, BF<sub>01</sub> = 8.72; within 16° of ±32°: AQ -  $\tau_b$  = -0.068, BF<sub>01</sub> = 2.86; RISC 225 -  $\tau_b = -0.129$ , BF<sub>01</sub> = 0.84; SPQ -  $\tau_b = 0.018$ , BF<sub>01</sub> = 5.45; within 24° of ±32°: AQ -  $\tau_b = 0.057$ , BF<sub>01</sub> = 226 11.67; RISC -  $\tau_b$  = -0.078, BF<sub>01</sub> = 2.40; SPQ -  $\tau_b$  = 0.006, BF<sub>01</sub> = 5.02). 227

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#### 230 Modeling results

231 Group level results

To quantitatively evaluate the relationships between underlying perceptual mechanisms and task performance we fitted a range of generative models. One class of models was Bayesian - it was based on the assumption that participants combine prior expectations with uncertain sensory information on a single trial basis (**Fig. 5**).

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Figure 5. Bayesian model of estimation response for a single trial. The actual motion direction ( $\theta_{act}$ ) is corrupted by sensory uncertainty ( $\sigma_{sens}$ ), and then combined with prior expectations (mean  $\theta_{exp}$  and uncertainty  $\sigma_{exp}$ ) to form a posterior distribution. The perceptual estimate ( $\theta_{perc}$ ) is defined as the mean of the posterior distribution. Finally, motor precision ( $1/\sigma_m^2$ ) and a probability of random response ( $\alpha$ ) are incorporated to generate the response ( $\theta_{est}$ ). This results in 4 free model parameters:  $\sigma_{sens'}$ ,  $\sigma_{exp}$ ,  $\theta_{exp}$  and  $\alpha$ . The motor precision is estimated from high contrast trials and is used as a fixed parameter.

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246 To account for the possibility that the bimodal probability distribution of the stimuli, in addition 247 to inducing prior expectations, has also affected the sensory likelihood, we constructed three 248 variations of the Bayesian model: 'BAYES', where the sensory precision was constrained to be the same across all presented motion directions, 'BAYES\_varmin', where the sensory precision 249 250 was allowed to be different for the most frequently presented motion directions, but was the same across all other directions, and 'BAYES\_var', where sensory precision was allowed to be 251 252 different across all motion directions. Another class of models was based on the assumption that 253 task performance can be explained by response strategies that do not involve Bayesian inference. 254 That is, on any given trial participants responded based on the prior expectations or sensory 255 information alone. We considered four variations of response strategy models: 'ADD1', 'ADD2', 'ADD1\_m' and 'ADD2\_m' (see Methods for details). 256

To compare the models, we computed BIC values for each individual for each model; we used
individual BIC values as a summary statistic and compared the models using signed rank test in
order to preserve individual variability, which corresponds to a random effects Bayesian model

selection procedure. We found that the BAYES model had significantly smaller BIC values thanthe remaining models (see the p-values within Fig. 6a).

To determine how the best fitting model compared to the actual data, we analyzed the estimation biases and variation in estimation responses as predicted by BAYES (**Fig. 6b,c**). As in the experimental data analysis, we computed estimation distributions predicted by the model by assuming occasional random estimations (see Eq. (2)). Finally, using the BAYES model, we reconstructed the priors acquired by participants. While on the individual level there was a considerable variation in the shape of acquired priors (see **Appendix 1–Figure 10**), on the group level, it approximated the statistics of the task (**Fig. 6d**).

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Figure 6: Modelling results. (a) Model comparison for all participants using Bayesian 271 Information Criterion (BIC). y-axis measures the relative difference between BIC of each 272 model (as indicated on the x-axis) and BIC of BAYES model. Values greater than zero on the 273 y-axis indicate that the BAYES model provided a better fit. Each dot represents a participant. 274275 Red horizontal lines denote median values; blue horizontal lines denote 25th and 75th percentiles. p-values above the plot indicate whether the median of the difference was 276 significantly different from zero for each model (signed rank test). Panels (a) and (c) present 277 task performance at different motion directions as predicted by BAYES model: (b) estimation 278 bias, (c) standard deviation of estimations. Error bars represent within-subject standard error. 279 (d) Population averaged prior as recovered via BAYES model. The vertical dashed lines 280 281 correspond to the two most frequently presented motion directions (±32°).

#### 283 Model parameters and autistic/schizotypal traits

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Correlational analysis of BAYES model parameters showed that there was no correlation between AQ and the precision of the prior  $\sigma \exp$  (**Fig. 7b**; *r* = 0.018, p = 0.962). That autistic traits had no effect on the precision of the prior was confirmed by Bayesian Kendall correlation, which provided positive evidence ( $\tau_b = 0.001$ , BF<sub>01</sub> = 6.99).

289 Importantly, autistic traits were found to be strongly associated with less uncertainty in the 290 sensory likelihood,  $\sigma$ sens (Fig. 7c; r = -0.185, p = 0.011), which also remained significant after 291 Bonferroni correction (p = 0.044). Finally, there was no correlation with the amount of random 292 estimations (Fig. 7d; r = -0.135, p = 0.238). Motor precision, which was estimated from high 293 contrast trials, separately from all other parameters (see Methods), was also correlated with 294 autistic traits (r = 0.245, p = 0.012). On the other hand, consistent with the absence of differences in the behavioral findings, schizotypal traits were not associated with any difference in the 295 296 BAYES model parameter values (Appendix 1–Figure 9), and in particular, were found to have no effect on prior precision (RISC:  $\tau_b = -0.012$ , BF<sub>01</sub> = 6.90; SPQ:  $\tau_b = 0.071$ , BF<sub>01</sub> = 3.97). 297

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Figure 7: Correlations between AQ scores and BAYES model parameters. (a)  $\theta_{exp}$  - mean of the prior expectations (r = 0.031, p = 0.820), (b)  $\sigma_{exp}$  - uncertainty of the prior distribution (r = 0.018, p = 0.962), (c)  $\sigma_{sens}$  - uncertainty in the sensory likelihood (r = -0.185, p = 0.011) and (d)  $\alpha$  - fraction of random estimations (r = -0.135, p = 0.238). The blue lines are robust regression slopes.

This zip archive contains .csv files with all of the data that was used to produce plots in Fig. 7. BayesEstimatedParams.csv contains BAYES model parameter estimates. Traits.csv contains AQ scores of each individual (column 3) as well as all other traits. SourceData\_Readme.txt contains more detailed description of each data file. The plots were produced with MATLAB script analyze\_params.m which is available in the provided Source Code File 1. The SourceCode\_Readme.txt contains more detailed description of the source code.

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#### 314 Parameter recovery for BAYES

315 Finally, to further investigate that in our experimental paradigm the influence of stronger likelihoods can be distinguished from that of weaker priors 10, 11 we performed parameter 316 317 recovery for the winning BAYES model. Parameter recovery involves generating synthetic data 318 with different sets of parameters ('actual parameters') and then fitting the same model to 319 estimate the parameters ('recovered parameters') that are most likely to have produced the data. If actual and recovered parameters are in a good agreement, it means that the effects of different 320 321 parameters can be reliably distinguished. At the same time, parameter recovery is also affected 322 by the parameter estimation methods and even more so by the amount of data used for model 323 fitting. Therefore, parameter recovery provides an overall check for the reliability of modelling 324 results and is recommended as an essential step in computational modelling approaches <sup>30</sup>.

We found that overall BAYES model (and MLE parameter estimation using simplex optimization function) recovered parameters very well, which was reflected in Pearson's correlation between actual and recovered estimates being r > 0.9 for all model parameters (**Fig. 8**).



Figure 8: Comparison of actual (x-axis) vs. recovered (y-axis) parameters using the 'BAYES' model. (a)  $\theta_{exp}$  - mean of the prior expectations (r = 0.90), (b)  $\sigma_{exp}$  - uncertainty of the prior distribution (r = 0.92), (c)  $\sigma_{sens}$  - uncertainty in the sensory likelihood (r = 0.95), (d)  $\alpha$  fraction of random estimations (r = 0.98). The dashed diagonal line is a reference line

#### indicating perfect parameter recovery.

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#### 336 Discussion

In this study, we investigated whether autistic and schizotypal traits are associated with 337 differences in the implicit Bayesian inference performed by the brain. Specifically, we wanted to 338 339 know whether autistic and schizotypal traits are accompanied by 1) differences in how the priors are updated and/or in their precision and/or by 2) differences in the precision with which 340 341 the sensory information (the likelihood) is represented. We used a visual motion estimation task 342 <sup>29</sup> that induces implicit prior expectations via more frequent exposure of two motion directions (±32°). We found that on the group level (N=83) participants acquired prior expectations 343 towards  $\pm 32^{\circ}$  motion directions. This was indicated by shorter estimation reaction times and 344 better detection at  $\pm 32^{\circ}$ , as well as attractive biases towards  $\pm 32^{\circ}$  and reduced estimation 345 variability at ±32°. Moreover, when no stimulus was presented, participants sometimes still 346 reported seeing the stimulus, mostly around  $\pm 32^{\circ}$ . Performance was best explained by a simple 347 348 Bayesian model, which provided a good fit to the data and captured the characteristic features of perceptual bias and variability. This model provided estimates of Bayesian priors and sensory 349 350 likelihoods for each participant, which were then analyzed in relation to participants' schizotypal and autistic traits. 351

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353 Schizotypal traits were found to have no measurable effect on perceptual biases in our task and, therefore, were not associated with any differences in the precision ascribed to priors and 354 355 likelihoods. This finding challenges recent accounts of positive symptoms of schizophrenia that 356 predict impaired updating of priors and an imbalance in precision ascribed to sensory information and prior expectations<sup>1-3</sup>. An immediate explanation might be that the influence of 357 schizotypal traits in the healthy population is not strong enough to lead to behavioral 358 359 differences, even if the dimensionality assumption holds. This would need to be addressed by further research investigating clinical populations. Another possibility is that the aberrant 360 perception subconstruct of schizotypal traits, for which we did not acquire explicit measures, is 361 more relevant for the hypothesized effects then the entire construct as a whole. For example, a 362 recent study by Powers et al<sup>31</sup> found that overweighing of perceptual priors was specifically 363

linked to hallucinatory propensity and not to the diagnostic status of psychosis itself. 364 Furthermore, Teufel et al.<sup>16</sup> also found that stronger influence of prior knowledge was primarily 365 associated with hallucinatory propensity and not with delusional propensity. Another possible 366 difference between Teufel et al.<sup>16</sup> study and ours might be the level at which the priors operate. 367 368 In Teufel et al.<sup>16</sup>, participants were presented with ambiguous two-tone versions of images 369 before and after seeing the actual images in full color and had to report whether the presented 370 two-tone image contains a face. The low-level prior for basic perceptual features (as induced in 371 our task) might function at a hierarchically lower level than prior knowledge related to complex 372 collection of features and semantic content (faces). The level at which prior expectations are 373 induced has indeed been shown to matter. A series of studies by Schmack et al.<sup>17, 27, 28</sup> using 3D 374 rotating cylinders report weaker low-level (perceptually-induced - stabilizing) priors but 375 stronger high-level (cognitively-induced) priors in both schizophrenia and schizotypal traits. It 376 is difficult to compare and reconcile these findings with ours. One possibility is that the priors 377 induced in our task lie in between their perceptual and cognitive levels. The taxonomy of priors in relation to their place in the computational hierarchy or to their complexity or specificity is 378 still far from being established <sup>32</sup> and thus the potential relevance of such distinctions is still not 379 380 known.

Autistic traits were associated with significant behavioral differences: weaker biases and lower variability of direction estimation on low contrast trials. Modeling revealed that this was because of increased sensory precision as well as higher motor precision, while there was no attenuation of acquired priors. Parameter recovery analysis confirmed that our methodology provides reliable parameter estimates and, in particular, allows disentangling variations in priors and likelihoods.

387 Autistic traits were also found to be associated with less false detections (hallucinations) on trials 388 when no stimulus was presented, consistent with the idea that prior expectations had less 389 influence in individuals with higher AQ. In an attempt to measure those individual differences, 390 we fitted a more sophisticated Bayesian model that could account not only for the estimation 391 performance but also for the detection data (see **Appendix 2**). This model provided a good fit to 392 both estimation and detection data, and preserved the correlation between ASD traits and the precision of the motion direction likelihood (r = -0.202, p = 0.029). However, parameter recovery 393 394 was not as good as for the BAYES model presented above (see Appendix 2 - Figure 3) and for this reason we focused on the simpler model in this paper. 395

Overall, our findings are in agreement with most of the recent Bayesian theories of ASD, namely, that autistic traits are associated with a relatively weaker influence of prior expectations. However, we find that this is due to enhanced sensory precision <sup>6,7,10,13</sup>, rather than attenuated priors per se<sup>4</sup>. Other empirical studies inspired by the Bayesian accounts have reported either attenuated or intact priors, but most are subject to methodological limitations, either because they did not use computational modeling <sup>15, 22,-24</sup> or because their model could not extract likelihoods and quantify their variations <sup>14,26</sup>.

403 The idea that sensory processing could be enhanced in autism has long been proposed outside 404 the Bayesian framework. Autistic traits have been associated with enhanced orientation 405 discrimination<sup>33</sup>, but only for first-order (luminance-defined) stimulus<sup>34</sup>. This enhancement has 406 been proposed to be a result of either enhanced lateral<sup>34</sup>, or a failure to attenuate sensory signals 407 via top-down gain control<sup>6</sup>, both of which could be directly related to narrower likelihoods in 408 the Bayesian framework<sup>35</sup>. However, in motion perception, previous research did not find 409 improved discrimination for first-order stimulus in autism, while for second-order (texture-410 defined) stimulus, the autistic group was found to underperform <sup>36</sup>. Our findings challenge these 411 results and call for more research in this area.

412 In ASD as in schizotypy, prior integration might function differently at different levels of sensory 413 processing. For example, Pell et al.<sup>23</sup> reported intact direction-of-gaze priors for healthy 414 individuals with high autistic traits and for highly functional individuals with a clinical 415 diagnosis. The authors did not directly investigate differences in sensory precision, but the lack of 416 behavioral differences suggests that there was none. Arguably, their paradigm involves more 417 complex stimuli than used in our task, which are also strongly associated with semantic content 418 (faces). It would not be surprising if increased sensory precision does not extend to such stimuli. 419 In fact, autistic individuals are known to exhibit differential performance based on the 420 complexity of the stimulus<sup>34</sup>, which also lies at the foundation of some theoretical accounts, such as the 'Weak Central Coherence' <sup>37</sup>. 421

In our paradigm people acquire prior expectations very quickly, within 200 trials (see Appendix 1), which did not allow us to study individual differences in the rate at which the priors are acquired. Bayesian accounts predict differences in the dynamical updating of the priors, namely, that both autistic and schizotypal traits should be associated with increased learning rate - which is the ratio of likelihood and posterior precisions <sup>7</sup>. Our findings of increased

427 sensory precision in autistic traits also suggest that their learning rate should be faster. However, 428 this prediction might need to be more nuanced for volatile environments when there are multiple 429 (hierarchical) levels of uncertainty that need to be updated simultaneously. A recent study by 430 Lawson et al.<sup>26</sup> found that when transitioning from stable to volatile environments, autistic adults 431 showed larger change in the learning rate about volatility and smaller change in the learning rate 432 about the environmental probabilities, while the average learning rates were found to not be 433 different from those of controls.

Another aspect that our paradigm could not test is the specificity of the acquired priors <sup>32</sup>. Some Bayesian accounts <sup>5</sup> predict that priors may be overly context-sensitive in autism. This is in line with the view that generalization is impaired in autism <sup>38</sup>. Furthermore, such over-specificity is thought to be stronger with more repetitive stimuli <sup>39</sup>. Future research could address this using statistical learning paradigms that incorporate increasingly distinct contexts or stimuli.

439

#### 440 Conclusion

441 We investigated statistical learning and Bayesian inference in a visual motion perception task 442 along autistic and schizotypal traits. To our knowledge, this study is the first to investigate 443 differences in Bayesian inference along both trait spectra in a single task. Furthermore, 444 this study is the first visual study to computationally disentangle and quantitatively 445 assess the variations in individuals' likelihoods and priors. Surprisingly, schizotypal traits were found to have no effect on task performance and thus were not associated with any 446 447 differences in the underlying statistical learning and Bayesian inference. For autistic traits, however, significant behavioral differences in prior integration were found, which were due to **448** 449 an increase in the precision of internal sensory representations in participants with higher AQ. 450 Whether the current results extend to clinical populations will have to be examined in the 451 future.

452

#### 453 Methods

454

#### 455 Participants

91 (47 females, 44 males, age range: 18-69) naïve participants with no motor disabilities and with
normal (or corrected to normal) vision were recruited from the general population. We
advertised for participants using posters and the internet across University of Edinburgh

459 locations and other sites across Edinburgh. All participants gave informed written consent and
460 received monetary compensation for participation. The study was approved by the University of
461 Edinburgh School of Informatics Ethics Panel.

462

#### 463 Questionnaires

464 ASD was assessed using 50-item version Autism Spectrum Quotient (AQ)<sup>40</sup>, which is commonly used for assessing milder variants of autistic-like traits within the general population. 465 466 Schizotypal traits were assessed using The Rust Inventory of Schizotypal Cognitions (RISC)<sup>41</sup>. RISC is specifically developed to measure schizotypal traits in the general population. In 467 468 addition, a sub-group of 41 participants also completed Schizotypal Personality Questionnaire 469 (SPQ)<sup>42</sup>. Finally, all participants were also asked to complete the Warwick-Edinburgh Mental Well-being Scale (WEMWBS)<sup>43</sup> in order to control for potential depression-induced differences 470 in performance <sup>44</sup>. 471

472

#### 473 Apparatus

The visual stimuli were generated using Matlab Psychophysics Toolbox <sup>45</sup>. Participants viewed the display in a dark room at a distance of 80-100cm. The stimuli consisted of a cloud of dots with a density of 2 dots/deg<sup>2</sup> moving coherently (100%) at a speed of 9°/sec. Dots appeared within a circular annulus with minimum diameter of 2.2° and maximum diameter of 7°. The stimuli were displayed on a Dell P790 monitor running at 1024×768 at 100 Hz. The display luminance was calibrated using a Cambridge Research Systems Colorimeter (ColorCal MKII).

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#### 482 The task

The task was developed previously in our laboratory <sup>29</sup>. Participants have to: i) estimate the direction of coherently moving simple stimuli (dots) that are presented at low contrast levels (estimation task) and then ii) indicate whether they have actually perceived the stimulus or not (detection task). Since Chalk et al.<sup>29</sup> had shown that the effects of acquired priors become significant within the first 200 trials, instead of two experimental sessions of 850 trials each as in the original study, we used a single session of 567 trials (lasting around 40 min).

Each trial started by first displaying a fixation point  $(0.5^{\circ}, 12.2 \text{ cd/m}^2)$  for 400 ms, after which a 489 field of moving dots appeared along with an orientation bar (length 1.1<sup>°</sup>, width 0.03<sup>°</sup>, luminance 490 491 4 cd/m<sup>2</sup>, extending from the fixation point). Initial angle of the bar was randomized for each 492 trial. Participants had to estimate the direction of motion by aligning the bar (using a computer 493 mouse) to the direction the dots were moving in, and by clicking the mouse button to validate 494 their estimate. The display cleared when either the participant had clicked the mouse or when 495 3000 ms had elapsed. On trials where no stimulus was presented, the bar still appeared for the 496 estimation task to be completed.

497 After a 200ms delay, the participants had to indicate whether they had actually detected the 498 presence of dots in the estimation period (detection task). The display was divided into two 499 parts by a vertical white line across the center of the screen, the left hand side area reading "NO 500 DOTS" and the right hand side area reading "DOTS" (Fig. 2a). The cursor appeared in the center 501 of the screen, and participants had to move it to the left or right and click to indicate their 502 response. Immediate feedback for correct or incorrect detection responses was given by a cursor 503 flashing green or red, respectively. The screen was cleared for 400 ms before the start of a new 504 trial. Every 20 trials, participants were presented with feedback on their estimation performance 505 in terms of average estimation error in degrees (e.g., "In the last 20 trials, your average estimation error was 23°"). Every 170 trials (i.e. on three occasions) participants were given a 506 507 chance to "have a short break to rest their eyes", in order to prevent fatigue. Participants clicked 508 when they were ready to continue.

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#### 512 Design

The stimuli were presented at four different levels of contrast: 0 contrast (no-stimulus trials), 2 low levels contrasts and high contrast, randomly mixed across trials. There were 167 trials with no stimulus. The 2 low levels of contrast were determined using 4/1 and 2/1 staircases on detection performance <sup>46</sup>. There were 243 trials following the 4/1 staircase and 90 trials following the 2/1 staircase. The remaining 67 trials were at high contrast, which was set to 3.51 cd/m<sup>2</sup> above the background luminance.

For the two low contrast levels, there was a predetermined number of possible directions:  $\vec{0}$ , 519  $\pm 16^{\circ}$ ,  $\pm 32^{\circ}$ ,  $\pm 48^{\circ}$ , and  $\pm 64^{\circ}$  with respect to a reference direction. The reference direction was 520 521 randomized for each participant. For the 2/1 staircased contrasts, each predetermined motion direction was presented equally frequently. Unbeknownst to participants, stimuli at high and 4/1 522 staircase contrasts were presented more frequently at  $-32^{\circ}$  and  $+32^{\circ}$  motion directions, resulting 523 in a bimodal probability distribution (Fig. 1b). For the 4/1 staircase contrast level, the dots 524 were moving at  $\pm 32^{\circ}$  in 173 (~70%) trials and in all the other predetermined motion directions in 525 the remaining 70 (~30%) trials equally frequently. At the highest contrast level, 34 (~50%) trials 526 had the dots moving at  $\pm 32^{\circ}$  and the remaining 33 (~50%) trials were at random directions (i.e. 527 not just the predetermined directions). 528

529

#### 530 Data analysis

Responses on high contrast trials were used as a performance benchmark to ensure that participants were performing the task adequately. The predefined inclusion criteria were: 1) at least 80% detection and 2) less than  $30^{\circ}$  root mean squared error of estimations. 8 out of 91 participants failed to satisfy at least one of the criteria and were excluded from further analysis (Appendix 1–Figure 1).

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537 Data analysis on the estimation of motion directions was performed on 4/1 and 2/1 staircased 538 contrast levels only and only on trials where participants both validated their choice with a click 539 within 3000 ms in the estimation part and clicked "DOTS" in the detection part. The first 170 540 trials of each session were excluded from the analysis, as this was the upper limit for the 541 convergence of the staircases to stable contrast levels (**Appendix 1–Figure 2**).

542

After removing these trials, the luminance levels achieved by the 2/1 and 4/1 staircases were
found to be considerably overlapping (Appendix 1–Figure 2). Therefore, the data for both of
these contrast levels was combined for all further analysis.

546 To account for random estimations (either accidental or intentional) that participants made on

some trials, we fitted each participant's estimation responses to the probability distribution:

548  $(1-\alpha) \cdot V(\theta \mid \mu, \kappa) + \alpha$ ,

549 Where  $\alpha$  is the proportion of trials in which participant makes random estimates, and  $V(\theta | \mu, \kappa)$ 550 is the probability density function for the estimated angle  $\theta$  for von Mises (circular normal) 551 distribution with the mean  $\mu$  and precision  $\kappa$ . The parameters  $\mu$  and  $\kappa$  of the von Mises 552 distribution were determined by maximizing the likelihood of the distribution in Eq. (2) for each 553 presented angle.

To analyze the distribution of estimations in no-stimulus trials, we constructed histograms of 16<sup>°</sup> size bins. These histograms were converted into probability distributions by normalizing over all motion directions. We analyzed the estimation distribution when participants reported seeing dots (clicked "DOTS") within no-stimulus trials. We interpreted these false alarms as a simple form of perceptual hallucination.

559

#### 560 Modelling

#### 561 Bayesian models

562 Bayesian models assume that participants combined a learned prior of the stimulus directions 563 with their sensory evidence in a probabilistic manner. We first assume that participants make 564 noisy sensory observations of the actual stimulus motion direction ( $\theta_{act}$ ), with a probability

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566 
$$p_{sens}(\theta_{sens} | \theta_{act}) = V(\theta_t, \kappa_{sens}).$$
 (3)

567

where  $\theta_t$  itself varies from trial to trial around  $\theta_{act}$  according to  $p(\theta_t | \theta_{act}) = V(\theta_{act}, \kappa_{sens})$ . While participants cannot access the "true" prior,  $p(\theta)$ , directly, we hypothesized that they learned an approximation of this distribution, denoted  $Pexp(\theta)$ . This distribution was parameterized as the sum of two von Mises distributions, centered on motion directions  $\theta_{exp}$ and  $-\theta_{exp}$ , and each with precision  $\kappa_{exp}$ :

573

574  $p_{exp}(\theta) = 0.5 \left[ V \left( -\theta_{exp}, \kappa_{exp} \right) + V(\theta_{exp}, \kappa_{exp}) \right]$ (4)

575

576 Combining these via Bayes' rule gives a posterior probability that the stimulus is moving in a 577 direction  $\theta$ : 578  $p_{\text{post}}(\theta | \theta_{\text{sens}}) \propto p_{\text{exp}}(\theta) \cdot p_{\text{sens}}(\theta_{\text{sens}} | \theta)$ 

(5)

579

The perceived direction,  $\theta$  perc, was taken to be the mean of the posterior distribution (almost identical results would be obtained by using the maximum instead). Finally, we accounted for motor precision and a possibility of random estimates on some trials via:

584 
$$p(\theta_{est} | \theta_{perc}) = (1 - \alpha) \cdot V(\theta_{perc}, \kappa_m) + \alpha,$$
 (6)

585

where  $\alpha$  is the proportion of trials in which participants make random estimates and  $\kappa_m$  is the motor precision.

Increased exposure to some motion directions might not only give rise to prior expectations, but also induce learning in the sensory likelihood function itself <sup>47,52</sup>. Therefore, we fitted two more model variants: 'BAYES\_var' where  $\kappa_{sens}$  varied with the stimulus direction (i.e. it took five different values for each of the angles: 0°, ±16°, ±32°, ±48°, ±64°) and 'BAYES\_varmin' where  $\kappa_{sens}$  was allowed to be different for ±32° but was the same for all other directions.

593

#### 594 Response strategy models

595 We wanted to test whether task behavior might be better explained by simple behavioral 596 strategies. This class of models assumed that on trials when participants were unsure about the 597 presented motion direction, they made an estimation based solely on prior expectations, while 598 on the remaining fraction of trials they made unbiased estimates based solely on sensory inputs. 599 The first model, 'ADD1', assumed that estimations derived from prior expectations were simply sampled from a learnt expected distribution,  $pexp(\theta)$  (see Chalk et al.<sup>29</sup> and **Appendix 2**). The 600 second model, 'ADD2', was just as 'ADD1' except when participants were unsure about the 601 stimulus motion direction, instead of sampling from the complete learned probability 602 distribution ranging from  $-180^{\circ}$  to  $+180^{\circ}$ , they effectively truncated this distribution on a trial by 603 trial basis and sampled from only one part of it, negative  $(-180^{\circ} \text{ to } 0^{\circ})$  or positive  $(0^{\circ} \text{ to } +180^{\circ})$ , 604 605 depending on which side of the distribution the actual stimulus occurred (see Chalk et al, 2010 and SI). We also considered slight variations of the 'ADD1' and 'ADD2' models, denoted 'ADD1\_m' and 'ADD2\_m' respectively. These were identical to 'ADD1' and 'ADD2' except from setting  $1/\kappa_{exp}$  to zero; that is, on trials when perceptual estimates were derived only from expectations, they were equal to the mode of the learnt distribution (i.e. no uncertainty).

610

#### 611 Parameter estimation

We used performance in high contrast trials to estimate motor precision,  $\kappa_{m}$ , for each individual. 612 We assumed that, for those trials, sensory uncertainty was close to zero. Motor precision was then 613 determined by fitting estimation responses to the distribution in Eq. (2) by replacing  $\mu$  with the 614 actual motion direction,  $\theta_{act}$ . The estimated motor precision was used in all subsequent model 615 fitting as a fixed parameter. The rest of the free parameters were estimated by fitting the response 616 data at the two low (staircased) contrast levels. For each model with a set of free parameters M, we 617 computed the probability distribution  $p(\theta_{est} | \theta_{act}; M)$  of making an estimate  $\theta_{est}$  given the 618 actual stimulus direction  $\theta_{act}$ . For the response strategy models, by definition, the p( $\theta_{est} | \theta_{act}$ ; 619 M) corresponds to average behavior in the task. 620

The parameters were estimated by maximizing the fit of the log likelihood function for the experimental data for each participant individually. The maximum likelihood was found using a simplex algorithm, using *fminsearchbnd* Matlab function. To avoid convergence at a local maximum we constructed a grid of initial Kexp and Ksens parameter values covering the range found in previous studies. We selected the resulting set of parameters that corresponded to the largest log-likelihood.

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#### 628 Model Comparison

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630 To compare the model fits we used Bayesian Information Criterion (BIC), which approximates
631 the log of model evidence<sup>48</sup>:

$$632 \quad -2 \cdot \log(P(D \mid M)) \approx BIC = -2 \cdot \log(P(D \mid M, \Theta)) + k \cdot \log(n), \tag{7}$$

633 where M is model, D is observed data and  $P(D|M, \hat{\Theta})$  is the likelihood of generating the 634 experimental data given the most likely set of parameters,  $\hat{\Theta}$ ; *k* is the number of model parameters and *n* is the number of data points (or equivalently, the number of trials). BIC
evaluates the model by how it fits the data by also penalizing for model complexity (number of
parameters); lower BIC score indicates a better model.

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#### 639 Parameter recovery

To determine whether the BAYES model can distinguish the effects of strong likelihoods from 640 those of weak priors <sup>10, 11</sup> and to evaluate the robustness of our methods, we performed 641 parameter recovery. First, we generated 80 sets of parameters (i.e. 80 synthetic individuals) by 642 randomly sampling each parameter from a Gaussian distribution centered on the mean value of 643 each parameter found in our sample (40° for  $\theta_{exp}$ , 15° for  $\sigma_{exp}$ , 10° for  $\sigma_{sens}$ , 0.06 for  $\alpha$  and 10° 644 for  $\sigma_{motor}$ ). Second, for each set of parameters, we simulated data for 200 trials with the 645 Bayesian model by randomly sampling from the estimation probability distribution. We used 200 646 647 simulated trials only, to match the empirical data (200 corresponds to the amount of experimental trials used for fitting, after excluding high contrast and zero contrast trials).<sup>1</sup> Finally, we fitted the 648 BAYES model to the simulated data. To evaluate the goodness of recovered parameters, we 649 computed Pearson's correlation between the actual parameters and the recovered parameters. 650

651

#### 652 Statistical tests

Due to the presence of outliers in many of the measures, we used robust regression techniques for measuring the presence and strength of the effects in our data. This was done using *robustfit* function in Matlab, which downweighs the influence of outliers in proportion to their distance from the regression line, which is computed via iteratively reweighted least squares (IRLS)<sup>53</sup>. For the loss function we used Huber function<sup>54</sup> with a tuning constant of 1.345, which corresponds to 95% estimator efficiency as compared to ordinary least squares.

Furthermore, we applied Bonferroni correction for multiple testing based on the number of independent hypotheses that we tested; that is, whether two personality traits, ASD and schizotypy, were associated with the two variables of interest, acquired priors and sensory likelihoods, - this resulted in 4 different hypotheses. Note that while the number of null hypothesis significance tests that we performed exceeds this number, the tests within each set

<sup>&</sup>lt;sup>1</sup> Simulating more trials would result in a better parameter recovery but the results would no longer be informative about the reliability of parameters estimated from empirical data.

concerning the same hypothesis were not independent (each test was based on derivative and/or
correlated values to those in the other tests within the same set), and thus would not have met
the independence assumption on which Bonferroni correction is based.

Finally, due to the limitations of frequentist statistics for accepting the null hypothesis, we
performed Bayesian correlation analysis and computed Bayesian Factors<sup>55</sup> for the null
hypothesis (BF<sub>01</sub>). This was done using JASP<sup>56</sup> (Version 0.8.6). Due to the presence of outliers,
this analysis was carried out using the non-parametric Kendall's Tau-b correlation coefficient.

671

#### 672 Source code and data

The source data of the main figures is provided. These include, figure 3—source data 1, figure 4—source data 1 and figure 7—source data 1. Source Code File 1 contains all the source code necessary to reproduce the figures. More detailed information about the source code is in SourceCode\_Readme.txt, while SourceData\_Readme.txt contains more details about the source data files.

678

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682

- 683 Competing financial interests
- 684 The authors declare no competing financial interests.
- 685
- 686 Appendix 1

687 688

#### 689 Exclusion criteria

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In order to ensure that participants performed adequately in the psychophysical task, we used predetermined performance criteria for inclusion into the study. Firstly, participants were required to detect the motion stimuli on more than 80% of trials with the high contrast motion stimuli and also make active estimates of the motion directions by clicking the mouse. Secondly, their average estimation performance on the high contrast stimuli had to be within 30° of the 696 correct angle. 8 out of 91 participants failed to satisfy at least one of the criteria: 2 participants
697 did not satisfy the first criteria, 4 did not satisfy the second criteria and 2 did not satisfy both of
698 the criteria (Appendix 1–Figure 1). These participants were excluded from further analysis.



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Appendix 1—Figure 1: Task performance at the highest contrast level and exclusion Criteria. Left panel: fraction of detected high contrast trials - quantified as the fraction of trials in which participants both validated their choice with a click within 3000 ms in the estimation part and reported seeing dots (clicked "DOTS") in the detection part. Right panel: root mean square error of estimations on high contrast trials. The dashed lines represent minimum performance criteria (more than 80% detection and less than 30° RMS error of estimations). Excluded participants are denoted by cross markers.

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#### 708 Staircased stimulus contrast levels

Appendix 1—Figure 2 describes the average convergence of the contrast staircases. Two groups 709 comprising our sample performed the task at different background contrast levels. For a 710 subgroup of 50 participants (left panel), the background luminance was set to 1.16 cd/m2 for the 711 712 other sub-group of 41 (right panel) it was set to 5.18 cd/m2. For both groups, contrast staircases 713 converged after 170 trials for both intermediate contrast levels, denoted with the vertical dashed 714 line. In both groups, 2/1 and 4/1 staircased contrasts were considerably overlapping: on average 2/1 being 0.20±0.04 cd/m<sup>2</sup> and 4/1 being 0.22±0.04 cd/m<sup>2</sup> above the 1.16 cd/m<sup>2</sup> background 715 luminance; and on average 2/1 being 0.42±0.05 cd/m<sup>2</sup> and 4/1 being 0.46±0.05 cd/m<sup>2</sup> above the 716 5.18 cd/m<sup>2</sup> background luminance. Thus, the two intermediate contrasts were combined for all 717 further data analysis. 718



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Appendix 1—Figure 2: Population averaged stimulus contrast relative to the background contrast for the 2/1 (red) and 4/1 (black) staircased contrast levels. Standard deviation is denoted by shaded areas with corresponding colors. The vertical dashed line marks 170 trials. Left panel: 44 participants (remaining after exclusion) that performed the task with the background luminance set to 1.16 cd/m<sup>2</sup>. Right panel: 39 participants (remaining after exclusion) that performed the task with the background luminance set to 5.18 cd/m<sup>2</sup>.

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#### 728 Combining the different background luminance levels

To compare the two sub-groups that performed the task at different background luminance levels, we performed Wilcoxon two-tailed rank sum test for all of the behavioral measures and none of them indicated any differences: mean absolute estimation bias (z = 0.652; ranksum = 1920; p = 0.514), mean variance of estimations (z = -0.406; ranksum = 1803; p = 0.685), total number of hallucinations (z = 0.128; ranksum = 1862; p = 0.898) number of hallucinations within 8° of ±32° (z = 0.870; ranksum = 1943; p = 0.384), mean estimation reaction time (z = 0.479; ranksum = 1901; p = 0.632). The two groups were therefore combined.

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#### 738 Temporal emergence of the impact of expectations

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We investigated how many trials it took for the acquired prior effects to impact behavior. First, we looked at estimation reaction times (RT) and compared mean RT of each individual at ±32° with mean RT at all other directions; we compared cumulative moving averages at every 30 trials (Appendix 1—Figure 3). We found that it took less than 90 trials for RT at ±32° to become significantly shorter than average RT at all other directions (Appendix 1—Figure 3 and p-values within).





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Appendix 1—Figure 3: Cumulative moving average of ratio of estimation reaction times at +32° vs average reaction times at all other directions. Red bars indicate median values and blue bars indicate 25th and 75th percentiles. p-values indicate whether RTs at  $\pm 32^{\circ}$  are significantly shorter than average RTs over all other directions (one-tailed Wilcoxon signed rank test).

Similarly, we looked at average detection performance and compared the fraction of trials in which stimulus was detected at ±32° with the mean fraction detected over all other presented directions; again, we compared cumulative moving averages at every 30 trials (Appendix 1– Figure 4). We found that it took less than 90 trials for detection at ±32° to become significantly better than average detection over all other presented directions (Appendix 1– Figure 4 and pvalues within).

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Appendix 1—Figure 4: Cumulative moving average of ratio of fraction of detected stimuli at  $\pm 32^{\circ}$  vs average fraction detected at all other directions. Red bars indicate median values and blue bars indicate 25th and 75th percentiles. p-values indicate whether fraction detected at  $\pm 32^{\circ}$  are significantly larger than average fraction detected over all other directions (one-tailed Wilcoxon signed rank test).

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Lastly, for trials where no stimulus was presented, we looked at how long it took participants to start hallucinating predominantly around  $\pm 32^{\circ}$  as opposed to all other possible directions. This was quantified as a probability ratio  $p_{rel}$ :

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$$p_{rel} = p(\theta_{est} = \pm 32(\pm 8)) \cdot N_{bins}, \qquad (1)$$

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where  $N_{bins}$  is the number of bins (45), each of size 16°. This probability ratio would be equal to 1 773 if participants were equally likely to estimate within 8° of ±32° as they were to estimate within 774 775 other bins. Again, we computed cumulative moving mean at every 30 trials (Appendix 1-776 Figure 5). For participants who did not report seeing dots at any direction within a given number of trials (i.e. zero total hallucinations) this probability ratio was undefined, therefore, 777 those individuals were omitted from significance test at that point. We found that it took less 778 than 210 trials for *p*<sub>rel</sub> to become significantly larger than 1 (Appendix 1–Figure 5 and p-values 779 within). 780

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Appendix 1—Figure 5: Cumulative moving average of ratio of fraction of detected stimuli at  $\pm 32^{\circ}$  vs average fraction detected at all other directions. Red bars indicate median values and blue bars indicate 25th and 75th percentiles. p-values indicate whether fraction detected at  $\pm 32^{\circ}$  are significantly larger than average fraction detected over all other directions (one-tailed Wilcoxon signed rank test).

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#### 790 Schizotypy traits and task performance

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Appendix 1—Figure 6 and Appendix 1—Figure 7 show task performance by groups which were
formed by splitting the sample on the median RISC and SPQ scores respectively. Appendix 1—
Figure 8 shows the correlations between RISC and SPQ scores and the corresponding
performance measures. There were no significant correlations with any of the measures.

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Appendix 1—Figure 6: Average group performance on low-contrast trials (a-d) and on trials with no stimulus (e) by groups split by median RISC score. (a) Mean estimation bias, (b) standard deviation of estimations, (c) estimation reaction time and (d) fraction of trials in which the stimulus was detected. (e) Distribution of hallucinations. The vertical dashed lines correspond to the two most frequently presented motion directions (±32°). Error bars and shaded areas represent within-subject standard error.



Appendix 1—Figure 7: Average group performance on low-contrast trials (a-d) and on trials with no stimulus (e) by groups split by median SPQ score. (a) Mean estimation bias, (b) standard deviation of estimations, (c) estimation reaction time and (d) fraction of trials in which the stimulus was detected. (e) Distribution of hallucinations. The vertical dashed lines correspond to the two most frequently presented motion directions (±32°). Error bars and shaded areas represent within-subject standard error.



Appendix 1—Figure 8: Correlations between personality traits, RISC (top row) and SPQ (bottom row) and task performance. There were no significant correlations with any of the measures: mean absolute bias (left column), mean estimation variability (middle column) and total number of hallucinations (right column). Robust correlation coefficients and p-values are indicated above each plot. The blue lines denote robust regression.

#### 833 Schizotypy traits and model parameters

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Appendix 1—Figure 9 shows the robust correlation analysis results between the BAYES model parameter estimates and schizotypy scores. There was no significant correlation with any of the parameters. Further Bayesian correlation analysis provided positive evidence that schizotypy traits had no effect on prior precision (RISC:  $\tau_b = -0.012$ , BF<sub>01</sub> = 6.90; SPQ:  $\tau_b = 0.071$ , BF<sub>01</sub> = 3.97).



841 Appendix 1—Figure 9: Correlations with the BAYES model parameter values and schizotypy 842 traits (as measured by both RISC and SPQ). First column:  $\theta_{exp}$ - mean of the prior expectations, 843 second column:  $\sigma_{exp}$ - uncertainty of the prior distribution, third column:  $\sigma_{sens}$ - uncertainty in 844 the sensory likelihood and fourth column:  $\alpha$  - fraction of random estimations. Robust 845 correlation coefficients and p-values are indicated above each plot. The blue lines denote 846 robust regression.

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#### 849 Individual priors recovered via BAYES model

- 850 Appendix 1—Figure 10 shows a representative sample of the priors we extracted for a number
- 851 of individuals, using the 'BAYES' model.



Appendix 1—Figure 10: A representative sample of prior expectations for each individual as reconstructed via 'BAYES' model. The dashed lines correspond to the two most frequently

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#### 858 Appendix 2

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#### 860 Response bias models

presented motion directions (±32°).

We wanted to account for the possibility that the task behavior might be better explained by simple behavioral strategies. This class of models assumed that on trials when participants were unsure about the presented motion direction they made an estimation based solely on prior expectations, while on the remaining fraction of trials they made unbiased estimates based solely on sensory input.

867 ADD1

868

The first model ('ADD1') assumed that when participants were unsure about which motion direction they had perceived, they made an estimate that was close to one of the two most frequently presented motion directions. In this model, on each trial, participants make a sensory observation of the stimulus motion direction,  $\theta_{obs}$ . We parameterize the probability of observing the stimulus to be moving in a direction  $\theta_{obs}$  by a von Mises (circular normal) distribution centered on the actual stimulus direction and with width determined by  $1/k_{sens}$ :

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$$p_{sens}(\theta_{sens} \mid \theta_{act}) = V(\theta_{act}, k_{sens})$$
(3)

877

878 On most trials, we assume that participants make a perceptual estimate of the stimulus motion 879 direction ( $\theta_{perc}$ ) that is based entirely on their sensory observation so that  $\theta_{perc} = \theta_{obs}$ . However, on 880 a certain proportion of trials, when participants are uncertain about whether a stimulus was 881 present or not, they resort to their expectations by making a perceptual estimate that is sampled 882 from a learned distribution,  $p_{exp}(\theta)$ . For simplicity, we parameterize this distribution as the sum 883 of two circular normal distributions, each with width determined by 1/kexp, and centered on motion directions  $-\theta_{exp}$  and  $\theta_{exp}$ , respectively. Finally, we accommodate for the fact that there will 884 885 be a certain amount of noise associated with moving the estimation bar to indicate which 886 direction the stimulus is moving in as well as allowing for a fraction of trials  $\alpha$ , where participants make estimates that are completely random. Thus, the estimation response  $\theta_{est}$  is related to the perceptual estimate  $\theta_{perc}$  via the equation:

889  $p(\theta_{est} | \theta_{perc}) = (1 - \alpha) * V(\theta_{perc}, k_m) + \alpha.$ (4)

Bringing all this together, the distribution of estimation responses for a single participant isgiven by:

 $p(\theta_{est} \mid \theta_{act}) = (1 - \alpha)[(1 - a(\theta))p_l(\theta_{obs} = \theta_{est} \mid \theta_{act}) + a(\theta)p_{exp}(\theta_{est})] * V(0, k_m) + \alpha.$ 

(5)

893

898

900

where the asterisk denotes a convolution and  $a(\theta)$  determines the proportion of trials that participants sampled from the expected distribution,  $p_{exp}(\theta)$ . The resulting 'ADD1' model has 9 free parameters  $\theta_{exp}$ ,  $k_{exp}$ ,  $a(\theta)$  (which can take a different value for each of the 5 angles: 0, ±16, ±32, ±48, ±64),  $k_{sens}$  and  $\alpha$ .

899 ADD2

The second model, 'ADD2', was just as 'ADD1' except that it had slightly more complex strategy for trials when participants were unsure about the stimulus motion direction: instead of sampling from the complete learned probability distribution ranging from  $-180^{\circ}$  to  $+180^{\circ}$  (Eq. (11)), they effectively truncated this distribution on a trial by trial basis and sampled from only one part of it, negative (-180 to  $0^{\circ}$ ) or positive (0 to  $+180^{\circ}$ ), depending on which side of the distribution the actual stimulus occurred. Incorporating this into the distribution of estimation responses gives:

908

909 
$$p(\theta_{est} \mid \theta_{act}) = (1-\alpha)[(1-a(\theta)-b(\theta))p_l(\theta_{obs} = \theta_{est} \mid \theta_{act}) + a(\theta)p_{expN}(\theta_{est}) + b(\theta)p_{expP}(\theta_{est})] * V(\theta_{est}) + \alpha . (6)$$

910

911 where asterisk (\*) denotes convolution;  $a(\theta)$  and  $b(\theta)$  determine the proportion of trials in which 912 participants sample from either anticlockwise or clockwise distributions  $p_{expN}(\theta)$  and  $p_{expP}(\theta)$ , 913 respectively.

914

915 In addition, we also considered slight variations of the 'ADD1' and 'ADD2' models, denoted 916 'ADD1\_m' and 'ADD2\_m' respectively. These were identical to 'ADD1' and 'ADD2' except from 917 setting  $1/k_{exp}$  to zero; that is, on trials when perceptual estimates were derived only from 918 expectations, they were equal to the mode of the learnt distribution (i.e. no uncertainty).

919

920 Non-symmetric prior models

The stimulus distribution is multimodal and symmetric. Learning such a distribution might be inherently difficult. We reasoned that some individual differences might lie in asymmetries of the acquired priors. Therefore, we explored an alternative parameterization of the acquired priors which allowed them to be asymmetrical. We allowed the two modes in the prior to have different position with respect to 0° and to have different amount of probability associated with each mode. This resulted in:

928 
$$p_{exp}(\theta) = (1 - \pi) \cdot V(\theta_{p}, \kappa_{exp}) + \pi \cdot V(\theta_{n}, \kappa_{exp})$$

929 (2)

921

where  $\pi$  ( $\in$  [0 1]) is a mixing parameter. Using this parameterization we fitted 'BAYES' model as described in the main text (thus, we denoted this alternative model as 'BAYES\_ $\pi$ '). The alternative parameterization did not result in a better BIC as compared to 'BAYES' model (p = 0.378, signed rank test). In addition, we performed parameter recovery to determine how robust 'BAYES\_ $\pi$ ' is and found that recovering the mixing parameter  $\pi$  was not very reliable (r=0.4), although other parameters retained most of their previous reliability (**Appendix 2–Figure 1**). We thus focused on the simpler model in the current study.





939 Appendix 2—Figure 1: Comparison of actual and recovered parameters via 'BAYES\_ $\pi$ ' model. 940  $\theta_p$  and  $\theta_n$ - positive and negative modes of the bimodal distribution of prior expectations,  $\sigma_{exp}$ -

941 uncertainty of the prior distribution,  $\sigma_{sens}$  uncertainty in the sensory likelihood,  $\alpha$  - fraction of 942 random estimations,  $\pi$  - mixing parameter responsible for the degree of bimodality. Actual 943 parameters are scattered along x-axis and recovered parameters are scattered along y-axis. The 944 dashed diagonal line is a reference line indicating perfect parameter recovery. Pearson's 945 correlation coefficients are indicated above each plot.

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#### 948 Full models (estimation + detection)

950 We have built a Bayesian model that incorporates both estimation and detection performance 951 ('BAYES\_full') in order to fully account for the task behavior. This time, the acquired priors 952 consisted of both the expectations about the direction of stimuli motion ( $\theta$ ) and the expectations 953 about whether stimulus is presented (s=1) or not (s=0). It was parameterized as:

954

$$p_{exp}(\theta, s) = \begin{cases} (1-b) \cdot \frac{1}{2\pi}, & \text{if } s = 0\\ b \cdot \frac{1}{2} [V(-\theta_{exp}, \kappa_{exp}) + V(\theta_{exp}, \kappa_{exp})], & \text{if } s = 1 \end{cases}$$

955 956

957 where parameter *b* accounts for a participant's average expectation that the stimulus will be 958 presented. Thus, we assumed that expectations about motion direction were uniform for when 959 no stimulus was expected. While the expectations about motion direction when the stimulus 960 was expected followed the bimodal probability distribution just as in the previous models.

On each trial, given the presented motion direction ( $\theta_{act}$ ) and the presence of the stimulus (s), 961 962 participants made sensory measurements  $p_{sens}(\theta_{sens}, s_{sens} | \theta_{act}, s)$ . For simplicity, we assumed that the 963 sensory probability of whether the stimulus was present ( $p_{sens}(s_{sens} | \theta_{act,s})$ ) was independent of the 964 sensory input about the motion direction ( $p_{sens}(\theta_{sens} | \theta_{act,s})$ ). We further assumed that  $s_{sens}$  was 965 independent of the presented motion direction  $\theta_{act}$ , as informed by 'BAYES\_var' model (that 966 allowed the sensory likelihood to vary based on the presented motion direction), which did not 967 produce a better fit. As before, the mean of the motion direction was allowed to fluctuate on 968 trial-by-trial basis, such that:

969

$$p(\theta \mid \theta_{act}) = V(\theta_{act}, \kappa_{sens}), \qquad (7)$$

970 where  $\kappa_{sens}$  is sensory precision. Given the estimate of the mean  $\theta$ , the sensory input  $\theta_{sens}$  is 971 represented with the associated uncertainty via:

977

980

$$p_{sens}(\theta_{sens} \mid \theta) = V(\theta, \kappa_{sens}).$$
(8)

974 Putting all this together, the sensory likelihood was expressed as:

975 
$$p_{sens}(\theta_{sens}, S_{sens} \mid \theta, s) = p_{sens}(\theta_{sens} \mid \theta, s)p(s_{sens} \mid s), \qquad (9)$$

976 where  $p_{sens}(\theta_{sens} | \theta_{act}, s)$  was parameterized as:

$$p_{sens}(\theta_{sens}|\theta_{act},s) = \begin{cases} \frac{1}{2\pi}, & \text{if } s = 0\\ V(\theta,\kappa_{sens}), & \text{if } s = 1 \end{cases}$$

978 where we assumed that sensory likelihood is uniform when no stimulus is presented. Finally, 979  $p_{sens}(s_{sens}|s)$  was parameterized as:

$$p_{sens}(s_{sens} = \{0, 1\} | s) = \begin{cases} \{1 - c, c\}, & \text{if } s = 0\\ \{1 - d, d\}, & \text{if } s = 1 \end{cases}$$

where parameter *c* is the average probability of detecting dots when they are not presented, and
parameter 'd' is the average probability of detecting dots when they are presented. Putting
together prior and likelihood, the resulting posterior probability distribution becomes:

984 
$$p_{post}(\theta, s \mid \theta_{sens}, s_{sens}) \propto p_{sens}(\theta_{sens} \mid \theta, s) \cdot p_{sens}(s_{sens} \mid s) \cdot p_{exp}(\theta, s) , \qquad (10)$$

With a given posterior participants could have performed detection task at least in two ways.One way is to maximize the posterior (i.e. to always choose the value of s that has higherprobability):

988

$$S_{perc} = \arg\max\left[p_{post}(s \mid \theta_{sens}, S_{sens})\right]$$
(11)

989

990 Another way is to perform probability matching and choose in accordance to the size of the991 probabilities:

$$s_{perc} = \begin{cases} 0 \ , & \text{if } p_{post}(s=0|\theta_{sens}, s_{sens}) > \eta \\ 1 \ , & \text{if } p_{post}(s=0|\theta_{sens}, s_{sens}) < \eta \end{cases}$$

992 993

994 where  $\eta \in [0 \ 1]$  and is drawn for each trial from a uniform distribution. We considered both of 995 these possibilities and implemented a variant of the model for each. Finally, just as in 'BAYES' 996 model, the motion direction percept was formed by taking the mean of the posterior:

$$\theta_{perc} = \int \theta \cdot p_{post}(\theta | \theta_{sens}, s_{sens}) \ d\theta = \frac{1}{Z} \int \theta \cdot \sum_{s} p_{exp}(\theta) \cdot p_{sens}(\theta_{sens} | \theta, s) \cdot p_{sens}(s_{sens} | s) \theta_{sens}$$
(12)  
999

1000 As previously, we accounted for motor precision and the lapse responses via:

$$p(\theta_{est} \mid \theta_{perc}) = (1 - \alpha) \cdot V(\theta_{perc}, \kappa_{motor}) + \alpha \cdot p_{exp}(\theta) * V(0, \kappa_{motor}).$$
(13)

In total, 'BAYES\_full' model had 7 free parameters. To fit the model, in addition to intermediate contrast trials, we also used no-stimulus trial data. The rest of the fitting procedure was the same as in the main text: we built a distribution of 1,000 posterior estimations for each presented angle and one more distribution of 1,000 posterior estimations for no stimulus trials.

We found that 'BAYES\_full' provided a good fit and captured the main features of both 1007 1008 estimation and detection performance (Appendix 2–Figure 2). As before, to test how reliable parameters estimated for 'BAYES\_full' model are, we performed parameter recovery. Just as for 1009 1010 'BAYES' parameter recovery described in the main text, we generated 80 sets of parameters and simulated 200 trials of data with 'BAYES\_full' model for each of them. Then we fitted 1011 1012 'BAYES\_full' to the simulated data. The results revealed that parameters 'd' and 'c' had very poor recovery (Appendix 2-Figure 3). We thus focused on the simpler model in the current 1013 1014 study.

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1018 Appendix 2—Figure 2: Task performance as predicted by the BAYES\_full model. Left panel: 1019 mean estimation bias at different motion directions. Middle panel: standard deviation of 1020 estimations at different motion directions. Right panel: fraction of detected stimuli at 1021 different motion directions. The dashed lines correspond to the two most frequently 1022 presented motion directions (±32°). Error bars represent within-subject standard error.

1023



Appendix 2-Figure 3: Comparison of actual and recovered parameters via 'BAYES\_full' 1025 model.  $\theta_{exp}$ - the mean of prior expectations of motion direction,  $\sigma_{exp}$ - uncertainty of the prior 1026 1027 expectations of motion direction,  $\sigma_{sens}$  - uncertainty in the sensory likelihood,  $\alpha$  - fraction of random estimations, b - prior expectation for dots being presented, c likelihood of detecting 1028 the dots when they are not presented, d - likelihood of detecting the dots when they are 1029 presented. Actual parameters are scattered along x-axis and recovered parameters are 1030 scattered along y-axis. The dashed diagonal line is a reference line indicating perfect 1031 parameter recovery. 1032

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