# 1 Title Page

**Bimodal Inference in Humans and Mice**

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# 1 2 Abstract

2 Perception is known to cycle through periods of enhanced and reduced sensitivity to external

3 information. Here, we asked whether such slow fluctuations arise as a noise-related epiphe-

4 nomenon of limited processing capacity or, alternatively, represent a structured mechanism

5 of perceptual inference. Using two large-scale datasets, we found that humans and mice

6 alternate between externally- and internally-oriented modes of sensory analysis. During

7 external mode, perception aligns more closely with the external sensory information, whereas

8 internal mode is characterized by enhanced biases toward perceptual history. Computational

9 modeling indicated that dynamic changes in mode are enabled by two interlinked factors:

10 (i), the integration of subsequent inputs over time and, (ii), slow anti-phase oscillations in

11 the perceptual impact of external sensory information versus internal predictions that are

12 provided by perceptual history. **We propose that between-mode fluctuations generate**

13 **unambiguous error signals that enable optimal inference in volatile environments.**

# 14 3 One sentence summary

15 Humans and mice fluctuate between external and internal modes of sensory processing.

16

17

# 18 4 Introduction

19 The capacity to respond to changes in the environment is a defining feature of life1–3.

20 Intriguingly, the ability of living things to process their surroundings fluctuates considerably

21 over time4,5. In humans and mice, perception6–12, cognition13 and memory14 cycle through

22 prolonged periods of enhanced and reduced sensitivity to external information, suggesting

23 that the brain detaches from the world in recurring intervals that last from milliseconds to

24 seconds and even minutes4. Yet breaking from external information is risky, as swift responses

25 to the environment are often crucial to survival.

26 What could be the reason for these fluctuations in perceptual performance11? First, periodic

27 fluctuations in the ability to parse external information11,15,16 may arise simply due to

28 bandwidth limitations and noise. Second, it may be advantageous to actively reduce the costs

29 of neural processing by seeking sensory information only in recurring intervals17, otherwise

30 relying on random or stereotypical responses to the external world. Third, spending time away

31 from the ongoing stream of sensory inputs may also reflect a functional strategy that facilitates

32 flexible behavior and learning18: Intermittently relying more strongly on information acquired

33 from past experiences may enable agents to build up stable internal predictions about the

34 environment despite an ongoing stream of external sensory signals19. By the same token,

35 recurring intervals of enhanced sensitivity to external information may help to detect changes

36 in both the state of the environment and the amount of noise that is inherent in sensory

37 encoding19.

38 In this work, we sought to elucidate whether periodicities in the sensitivity to external

39 information represent an epiphenomenon of limited processing capacity or, alternatively,

40 result from a structured and adaptive mechanism of perceptual inference. To this end, we

41 analyzed two large-scale datasets on perceptual decision-making in humans20 and mice21.

42 **When less sensitive to external stimulus information, humans and mice did**

43 **not behave more randomly, but showed stronger serial dependencies in their**

44 **perceptual choices22–33.** These serial dependencies may be understood as driven by internal

45 predictions that reflect the autocorrelation of natural environments34 and bias perception

46 toward preceding experiences30,31,35. Computational modeling indicated that ongoing changes

47 in perceptual performance may be driven by systematic fluctuations between externally- and

48 internally-oriented *modes* of sensory analysis. **We suggest that such *bimodal inference***

49 **may help to build stable internal representations of the sensory environment**

50 **despite an ongoing stream of sensory information.**

51 **5 Results**

## 52 5.1 Human perception fluctuates between epochs of enhanced and

53 **reduced sensitivity to external information**

54 We began by selecting 66 studies from the Confidence Database20 that investigated how

55 human participants (N = 4317) perform binary perceptual decisions (Figure 1A; see Methods

56 for details on inclusion criteria). As a metric for perceptual performance (i.e., the sensitivity

57 to external sensory information), we asked whether the participant’s response and the

58 presented stimulus matched (*stimulus-congruent* choices) or differed from each other (*stimulus-*

59 *incongruent* choices; Figure 1B and C) in a total of 21*.*05 million trials.

60 In a first step, we asked whether the ability to accurately perceive sensory stimuli is constant

61 over time or, alternatively, fluctuates in periods of enhanced and reduced sensitivity to

62 external information. We found perception to be stimulus-congruent in 73.46% ± 0.15%

63 of trials (mean ± standard error of the mean; Figure 2A), which was highly consistent

64 across the selected studies (Supplemental Figure S1A). **In line with previous work8, we**

65 **found that the probability of stimulus-congruence was not independent across**

66 **successive trials: At the group level, stimulus-congruent perceptual choices were**

67 **significantly autocorrelated for up to 15 trials (Figure 2B), controlling for task**

68 **difficulty and the sequence of presented stimuli (Supplemental Figure 2A-B).**

69 At the level of individual participants, the autocorrelation of stimulus-congruence exceeded the

70 respective autocorrelation of randomly permuted data within an interval of 3*.*24 ± 2*.*39 *×* 10*−*3

71 trials (Figure 2C). In other words, if a participant’s experience was congruent (or incongruent)

72 with the external stimulus information at a given trial, her perception was more likely to

73 remain stimulus-congruent (or -incongruent) for approximately 3 trials into the future. **The**

74 **autocorrelation of stimulus-congruence was corroborated by logistic regression**

75 **models that successfully predicted the stimulus-congruence of perception at the**

76 **index trial** *t* = 0 **from the stimulus-congruence at the preceding trials within a**

77 **lag of 16 trials (Supplemental Figure S3).**

78 These results confirm that the ability to process sensory signals is not constant over time but

79 unfolds in multi-trial epochs of enhanced and reduced sensitivity to external information8.

80 As a consequence of this autocorrelation, the dynamic probability of stimulus-congruent

81 perception (i.e., computed in sliding windows of ± 5 trials; Figure 1C) fluctuated considerably

82 within participants (average minimum: 35.46% ± 0.22%, maximum: 98.27% ± 0.07%). In

83 line with previous findings9, such fluctuations in the sensitivity to external information had a

84 power density that was inversely proportional to the frequency in the slow spectrum11 (power

85 ~ 1/*fβ*, *β* = *−*1*.*32 ± 3*.*14 *×* 10*−*3, T(1*.*84 *×* 105) = *−*419*.*48, p < 2*.*2 *×* 10*−*308; Figure 2D).

86 This feature, which is also known as a ***1/f power law***36,37, represents a characteristic of

87 scale-free fluctuations in complex dynamic systems such as the brain38 and the cognitive

88 processes it entertains9,10,13,39,40.

## 89 5.2 Humans fluctuate between external and internal modes of

90 **sensory processing**

91 In a second step, we sought to explain why perception cycles through periods of enhanced and

92 reduced sensitivity to external information4. We reasoned that observers may intermittently

93 rely more strongly on internal information, i.e., on predictions about the environment that

94 are constructed from previous experiences19,31.

95 In perception, *serial dependencies* represent one of the most basic internal predictions that

96 cause perceptual decisions to be systematically biased toward preceding choices22–33. Such

97 effects of perceptual history mirror the continuity of the external world, in which the recent

98 past often predicts the near future30,31,34,35,41. Therefore, as a metric for the perceptual

99 impact of internal information, we computed whether the participant’s response at a given

100 trial matched or differed from her response at the preceding trial (*history-congruent* and

101 *history-incongruent perception*, respectively; Figure 1B and C).

102 First, we confirmed that perceptual history played a significant role in perception despite the

103 ongoing stream of external information. With a global average of 52.7% ± 0.12% history-

104 congruent trials, we found a small but highly significant perceptual bias towards preceding

105 experiences (*β* = 16*.*18 ± 1*.*07, T(1*.*09 *×* 103) = 15*.*07, p = 10*−*46; Figure 2A) that was largely

106 consistent across studies (Supplemental Figure 1B) and more pronounced in participants who

107 were less sensitive to external sensory information (Supplemental Figure 1C). Importantly,

108 history-congruence was not a corollary of the sequence of presented stimuli: History-congruent

109 perceptual choices were more frequent at trials when perception was stimulus-incongruent

110 (56.03% ± 0.2%) as opposed to stimulus-congruent (51.77% ± 0.11%, *β* = *−*4*.*26 ± 0*.*21,

111 T(8*.*57 *×* 103) = *−*20*.*36, p = 5*.*28 *×* 10*−*90; Figure 2A, lower panel). Despite being adaptive

112 in autocorrelated real-world environments19,34,35,42, perceptual history thus represented a

113 **source of bias** in the randomized experimental designs studied here24,28,30,31,43. **These**

114 **serial biases were effects of choice history, i.e., driven by the experiences reported**

115 **at the preceding trial, and could not be attributed to stimulus history, i.e., to**

116 **effects of the stimuli presented at the preceding trial (Supplemental Section 1.1).**

117 Second, we asked whether perception cycles through multi-trial epochs during which perception

118 is characterized by stronger or weaker biases toward preceding experiences. **In close**

119 **analogy to stimulus-congruence, we found history-congruence to be significantly**

120 **autocorrelated for up to 21 trials (Figure 2B), while controlling for task difficulty**

121 **and the sequence of presented stimuli (Supplemental Figure 2A-B).** In individual

122 participants, the autocorrelation of history-congruence was elevated above randomly permuted

123 data for a lag of 4*.*87 ± 3*.*36 *×* 10*−*3 trials (Figure 2C), confirming that the autocorrelation of

124 history-congruence was not only a group-level phenomenon. The autocorrelation of history-

125 congruence was corroborated by logistic regression models that successfully predicted the

126 history-congruence of perception at an index trial *t* = 0 from the history-congruence at the

127 preceding trials within a lag of 17 trials (Supplemental Figure S3).

128 Third, we asked whether the impact of internal information fluctuates as **a scale-invariant**

129 **process with a 1/f power law (i.e., the feature typically associated with fluctuations**

130 **in the sensitivity to external information**9,10,13,39,40). The dynamic probability of history-

131 congruent perception (i.e., computed in sliding windows of ± 5 trials; Figure 1C) varied

132 considerably over time, ranging between a minimum of 12.77% ± 0.14% and a maximum

133 92.23% ± 0.14%. In analogy to stimulus-congruence, we found that history-congruence

134 fluctuated as at power densities that were inversely proportional to the frequency in the

135 slow spectrum11 (power ~ 1/*fβ*, *β* = *−*1*.*34 ± 3*.*16 *×* 10*−*3, T(1*.*84 *×* 105) = *−*423*.*91, p <

136 2*.*2 *×* 10*−*308; Figure 2D).

137 Finally, we ensured that fluctuations in stimulus- and history-congruence are linked to each

138 other. When perceptual choices were less biased toward external information, participants

139 relied more strongly on internal information acquired from perceptual history (and vice

140 versa, *β* = *−*0*.*05 ± 5*.*63 *×* 10*−*4, T(2*.*1 *×* 106) = *−*84*.*21, p < 2*.*2 *×* 10*−*308, **controlling for**

141 **fluctuations in general response biases**; Supplemental Section 1.2). Thus, while sharing

142 the **1/f power law** characteristic, fluctuations in stimulus- and history-congruence were

143 shifted against each other by approximately half a cycle and showed a squared coherence

144 of 6*.*49 ± 2*.*07 *×* 10*−*3% (Figure 2E and F; we report the average phase and coherence for

145 frequencies below 0.1 1*/Ntrials*; see Methods for details).

146 In sum, our analyses indicate that perceptual decisions may result from a competition between

147 external sensory signals with internal predictions provided by perceptual history. We show

148 that the impact of these external and internal sources of information is not stable over time,

149 but fluctuates systematically, emitting overlapping autocorrelation curves and antiphase 1/f

150 profiles.

151 These links between stimulus- and history-congruence suggest that the fluctuations in the

152 impact of external and internal information may be generated by a unifying mechanism that

153 causes perception to alternate between two opposing *modes*18 (Figure 1D): During *external*

154 *mode*, perception is more strongly driven by the available external stimulus information.

155 Conversely, during *internal mode*, participants rely more heavily on internal predictions

156 that are implicitly provided by preceding perceptual experiences. The fluctuations in the

157 degree of bias toward external versus internal information created by such *bimodal inference*

158 may thus provide a novel explanation for ongoing fluctuations in the sensitivity to external

159 information4,5,18.

## 160 5.3 Internal and external modes of processing facilitate response

161 **behavior and enhance confidence in human perceptual decision-**

162 **making**

163 **The above results point to systematic fluctuations in the *decision variable*44**

164 **that determines perceptual choices, causing enhanced sensitivity to external**

165 **stimulus information during external mode and increased biases toward preceding**

166 **choices during internal mode. As such, fluctuations in mode should influence**

167 **downstream aspects of behavior and cognition that operate on the perceptual**

168 **decision variable44. To test this hypothesis with respect to motor behavior and**

169 **metacognition, we asked how bimodal inference relates to response times (RTs)**

170 **and confidence reports.**

171 With respect to RTs, we observed faster responses for stimulus-congruent as opposed to

172 stimulus-incongruent choices (*β* = *−*0*.*14 ± 1*.*6*×*10*−*3, T(1*.*99*×*106) = *−*85*.*84, p < 2*.*2*×*10*−*308;

173 Figure 2G). Intriguingly, whilst controlling for the effect of stimulus-congruence, we found

174 that history-congruent (as opposed to history-incongruent) choices were also characterized by

175 faster responses (*β* = *−*9*.*56 *×* 10*−*3 ± 1*.*37 *×* 10*−*3, T(1*.*98 *×* 106) = *−*6*.*97, p = 3*.*15 *×* 10*−*12;

176 Figure 2G).

177 When analyzing the speed of response against the mode of sensory processing (Figure 2H),

178 we found that RTs were shorter during externally-oriented perception (*β*1 = *−*11*.*07 ± 0*.*55,

179 T(1*.*98 *×* 106) = *−*20*.*14, p = 3*.*17 *×* 10*−*90). Crucially, as indicated by a quadratic relationship

180 between the mode of sensory processing and RTs (*β*2 = *−*19*.*86 ± 0*.*52, T(1*.*98 *×* 106) =

181 *−*38*.*43, p = 5 *×* 10*−*323), participants became faster at indicating their perceptual decision

182 when biases toward both internal and external mode grew stronger.

183 In analogy to the speed of response, confidence was higher for stimulus-congruent as opposed

184 to stimulus-incongruent choices (*β* = 0*.*04 ± 1*.*18 *×* 10*−*3, T(2*.*06 *×* 106) = 36*.*85, p =

185 3*.*25 *×* 10*−*297; Figure 2I). Yet whilst controlling for the effect of stimulus-congruence, we found

186 that history-congruence also increased confidence (*β* = 0*.*48 ± 1*.*38 *×* 10*−*3, T(2*.*06 *×* 106) =

187 351*.*54, p < 2*.*2 *×* 10*−*308; Figure 2I).

188 When depicted against the mode of sensory processing (Figure 2J), subjective confidence was

189 indeed enhanced when perception was more externally-oriented (*β*1 = 92*.*63 ± 1, T(2*.*06 *×* 106)

190 = 92*.*89, p < 2*.*2 *×* 10*−*308). Importantly, however, participants were more confident in their

191 perceptual decision for stronger biases toward both internal and external mode (*β*2 = 39*.*3 ±

192 0*.*94, T(2*.*06 *×* 106) = 41*.*95, p < 2*.*2 *×* 10*−*308). In analogy to RTs, subjective confidence thus

193 showed a quadratic relationship to the mode of sensory processing (Figure 2J).

194 Consequently, our findings predict that human participants lack full metacognitive insight

195 into how strongly external signals and internal predictions contribute to perceptual decision-

196 making. Stronger biases toward perceptual history thus lead to two seemingly contradictory

197 effects, more frequent errors (Supplemental Figure 1C) and increasing subjective confidence

198 (Figure 2I-J). This observation generates an intriguing prediction regarding the association of

199 between-mode fluctuations and perceptual metacognition: Metacognitive efficiency should be

200 lower in individuals who spend more time in internal mode, since their confidence reports are

201 less predictive of whether the corresponding perceptual decision is correct. We computed each

202 participant’s M-ratio45 (meta-d’/d’ = 0.85 ± 0.02) to probe this hypothesis independently

203 of inter-individual differences in perceptual performance. Indeed, we found that biases

204 toward internal information (as defined by the average probability of history-congruence) were

205 stronger in participants with lower metacognitive efficiency (*β* = *−*2*.*98 *×* 10*−*3 ± 9*.*82 *×* 10*−*4,

206 T(4*.*14 *×* 103) = *−*3*.*03, p = 2*.*43 *×* 10*−*3).

207 In sum, the above results indicate that reporting behavior and metacognition do not map

208 linearly onto the mode of sensory processing. Rather, they suggest that slow fluctuations in the

209 respective impact of external and internal information are most likely to affect perception at

210 an early level of sensory analysis46,47. Such low-level processing may thus integrate perceptual

211 history with external inputs into a decision variable44 that influences not only perceptual

212 choices, but also the speed and confidence at which they are made.

213 **In what follows, we probe alternative explanations for between-mode fluctuations,**

214 **test for the existence of modes in mice, and propose a predictive processing model**

215 **that explains fluctuations in mode ongoing shifts in the precision afforded to**

216 **external sensory information relative to internal predictions driven by perceptual**

217 **history.**

## 218 5.4 Fluctuations between internal and external mode cannot be

219 **reduced to general response biases or random choices**

220 **The core assumption of bimodal inference - that ongoing changes in the sensitivity**

221 **to external information are driven by internal predictions induced via perceptual**

222 **history - needs to be contrasted against two alternative hypotheses: When making**

223 **errors, observers may not engage with the task and respond stereotypically, i.e.,**

224 **exhibit stronger general biases toward one of the two potential outcomes, or**

225 **simply choose randomly.**

226 **Logistic regression confirmed that perceptual history made a significant contri-**

227 **bution to perception (***β* **=** 0*.*11 ± 5*.*79 *×* 10*−*3**, z =** 18*.*53**, p =** 1*.*1 *×* 10*−*76**) over and**

228 **above the ongoing stream of external sensory information (***β* **=** 2*.*2 ± 5*.*87 *×* 10*−*3**,**

229 **z =** 375*.*11**, p <** 2*.*2 *×* 10*−*308**) and general response biases toward (***β* **=** 15*.*19 ± 0*.*08**,**

230 **z =** 184*.*98**, p <** 2*.*2 *×* 10*−*308**).**

231 **When eliminating perceptual history as a predictor of individual choices at**

232 **individual trials, Akaike Information Criterion (AIC48) increased by** *δAIC* **=**

233 1*.*64*×*103 **(see Supplemental Figure S4A-B for parameter- and model-level inference**

234 **at the level of individual observers). Likewise, when eliminating slow fluctuations**

235 **in history-congruence as a predictor of slow fluctuations in stimulus-congruence**

236 **across trials, we observed an increase in AIC by** *δAIC* **=** 7*.*06 *×* 103**. These results**

237 **provided model-level evidence against the null hypotheses that fluctuations in**

238 **stimulus-congruence are driven exclusively by choice randomness or general**

239 **response bias (see Supplemental Section 1.2 and Supplemental Figure S5 for an**

240 **in-depth assessment of general response bias).**

241 **To confirm that changes in the sensitivity to external information are indicative of**

242 **internal mode processing, we estimated full and history-dependent psychometric**

243 **curves during internal, external, and across modes21. If, as we hypothesized,**

244 **internal mode processing reflects an enhanced impact of perceptual history,**

245 **one would expect a history-dependent increase in biases and lapses as well as a**

246 **history-independent increase in threshold. Conversely, if internal mode processing**

247 **were driven by random choices, one would expect a history-independent increase**

248 **in lapses and threshold, and no change in bias. In line with our prediction, we**

249 **found that internal mode processing was associated with a history-dependent**

250 **increase in bias and lapse as well as a history-independent increase in threshold**

251 **(Supplemental Section 1.3.1 and Supplemental Figure S6). This confirmed that**

252 **internal mode processing is indeed driven by an enhanced impact of perceptual**

253 **history.**

254 **In line with this, the quadratic relationship between mode and confidence (Figure**

255 **2J) suggested that biases toward internal information do not reflect a post-**

256 **perceptual strategy of repeating preceding choices when the subjective confidence**

257 **in the perceptual decision is low. Moreover, while responses became faster with**

258 **longer exposure to the experiments of the Confidence database, the frequency of**

259 **history-congruent choices increased over time, speaking against the proposition**

260 **that participants stereotypically repeat preceding choices when not yet familiar**

261 **with the experimental task (Supplemental Section 1.4.1).**

262 **Taken together, our results thus argue against recurring intervals of low task**

263 **engagement, which may be signaled by stereotypical or random responses, as an**

264 **alternative explanation for the phenomenon that we identify as bimodal inference.**

## 265 5.5 Mice fluctuate between external and internal modes of sensory

266 **processing**

267 In a prominent functional explanation for serial dependencies22–28,32,33,46, perceptual history

268 is cast as an internal prediction that leverages the temporal autocorrelation of natural

269 environments for efficient decision-making30,31,34,35,41. Since this autocorrelation is one of

270 the most basic features of our sensory world, fluctuating biases toward preceding perceptual

271 choices should not be a uniquely human phenomenon.

272 To test whether externally- and internally-oriented modes of processing exist beyond the

273 human mind, we analyzed data on perceptual decision-making in mice that were extracted

274 from the International Brain Laboratory (IBL) dataset21. We restricted our analyses to the

275 *basic* task21, in which mice responded to gratings of varying contrast that appeared either

276 in the left or right hemifield of with equal probability. We excluded sessions in which mice

277 did not respond correctly to stimuli presented at a contrast above 50% in more than 80% of

278 trials (see Methods for details), which yielded a final sample of N = 165 adequately trained

279 mice that went through 1*.*46 million trials.

280 We found perception to be stimulus-congruent in 81.37% ± 0.3% of trials (Figure 3A, upper

281 panel). In line with humans, mice were biased toward perceptual history in 54.03% ± 0.17%

282 of trials (T(164) = 23.65, p = 9*.*98 *×* 10*−*55; Figure 3A and Supplemental Figure S1D). Since

283 the *basic* task of the IBL dataset presented stimuli at random in either the left or right

284 hemifield21, we expected stronger biases toward perceptual history to decrease perceptual

285 performance. Indeed, history-congruent choices were more frequent when perception was

286 stimulus-incongruent (61.59% ± 0.07%) as opposed to stimulus-congruent (51.81% ± 0.02%,

287 T(164) = 31.37, p = 3*.*36 *×* 10*−*71; T(164) = 31.37, p = 3*.*36 *×* 10*−*71; Figure 3A, lower panel),

288 confirming that perceptual history was a **source of bias**24,28,30,31,43 as opposed to a feature

289 of the experimental paradigm.

290 **At the group level, we found significant autocorrelations in both stimulus-**

291 **congruence (42 consecutive trials) and history-congruence (8 consecutive trials;**

292 **Figure 3B), while controlling for the respective autocorrelation of task difficulty**

293 **and external stimulation (Supplemental Figure 2C-D).** In contrast to humans, mice

294 showed a negative autocorrelation coefficient of stimulus-congruence at trial 2, which was

295 due to a feature of the experimental design: Errors at a contrast above 50% were followed by

296 a high-contrast stimulus at the same location. Thus, stimulus-incongruent choices on easy

297 trials were more likely to be followed by stimulus-congruent perceptual choices that were

298 facilitated by high-contrast visual stimuli21.

299 At the level of individual mice, autocorrelation coefficients were elevated above randomly

300 permuted data within a lag of 4.59 ± 0.06 trials for stimulus-congruence and 2.58 ± 0.01 trials

301 for history-congruence (Figure 3C). **We corroborated these autocorrelations in logistic**

302 **regression models that successfully predicted the stimulus-/history-congruence**

303 **of perception at the index trial** *t* = 0 **from the stimulus-/history-congruence**

304 **at the 33 preceding trials for stimulus-congruence and 8 preceding trials for**

305 **history-congruence (Supplemental Figure S3)**. In analogy to humans, mice showed

306 anti-phase 1/f fluctuations in the sensitivity to internal and external information (Figure

307 3D-F).

308 **The above results confirm that fluctuations between internally- and externally-**

309 **biased modes generalize to perceptual decision-making in mice. Following our**

310 **hypothesis that bimodal inference operates at the level of perception, we predicted**

311 **that between-mode fluctuations modulate a decision variable44 that determines**

312 **not only perceptual choices, but also downstream aspects of mouse behavior44.**

313 We therefore asked how external and internal modes relate to the trial duration (TD, a

314 coarse measure of RT in mice that spans the interval from stimulus onset to feedback21).

315 Stimulus-congruent (as opposed to stimulus-incongruent) choices were associated with shorter

316 TDs (*δ* = *−*262*.*48 ± 17*.*1, T(164) = -15.35, p = 1*.*55 *×* 10*−*33), while history-congruent choices

317 were characterized by longer TDs (*δ* = 30*.*47 ± 5*.*57, T(164) = 5.47, p = 1*.*66 *×* 10*−*7; Figure

318 3G).

319 Across the full spectrum of the available data, TDs showed a linear relationship with the

320 mode of sensory processing, with shorter TDs during external mode (*β*1 = *−*4*.*16 *×* 104 ±

321 1*.*29 *×* 103, T(1*.*35 *×* 106) = *−*32*.*31, p = 6*.*03 *×* 10*−*229, Figure 3H). However, an explorative

322 post-hoc analysis limited to TDs that differed from the median TD by no more than 1.5 x

323 MAD (median absolute distance49) indicated that, when mice engaged with the task more

324 swiftly, TDs did indeed show a quadratic relationship with the mode of sensory processing

325 (*β*2 = *−*1*.*97 *×* 103 ± 843*.*74, T(1*.*19 *×* 106) = *−*2*.*34, p = 0*.*02, Figure 3I).

326 As in humans, it is important to ensure that ongoing changes in the sensitivity to external

327 information are indeed driven by perceptual history and cannot be reduced to general choice

328 biases or random behavior. Logistic regression confirmed a significant effect perceptual

329 history on perceptual choices (*β* = 0*.*51 ± 4*.*49 *×* 10*−*3, z = 112*.*84, p < 2*.*2 *×* 10*−*308),

330 while controlling for external sensory information (*β* = 2*.*96 ± 4*.*58 *×* 10*−*3, z = 646*.*1, p <

331 2*.*2 *×* 10*−*308) and general response biases toward one of the two outcomes (*β* = *−*1*.*78 ± 0*.*02,

332 z = *−*80*.*64, p < 2*.*2 *×* 10*−*308). **When eliminating perceptual history as a predictor of**

333 **individual choices, AIC increased by** *δAIC* **=** 1*.*48 *×* 104**, arguing against the notion**

334 **that choice randomness and general response bias are the only determinants of**

335 **perceptual performance in mice (see Supplemental Figure S4C-D for parameter-**

336 **and model-level inference in individual subjects).**

337 **In mice, fluctuations in the strength of history-congruent biases had a significant**

338 **effect on stimulus-congruence (***β*1 **=** *−*0*.*12 ± 7*.*17 *×* 10*−*4**, T(**1*.*34 *×* 106**) =** *−*168*.*39**, p**

339 **<** 2*.*2 *×* 10*−*308**) beyond the effect of ongoing changes in general response biases**

340 **(***β*2 **=** *−*0*.*03 ± 6*.*94 *×* 10*−*4**, T(**1*.*34 *×* 106**) =** *−*48*.*14**, p <** 2*.*2 *×* 10*−*308**). Eliminating**

341 **the dynamic fluctuations in history-congruence as a predictor of fluctuations**

342 **in stimulus-congruence resulted in an increase in AIC by** *δAIC* **=** 2*.*8 *×* 104 **(see**

343 **Supplemental Section 1.2 and Supplemental Figure S5 for an in-depth assessment**

344 **of general response bias).**

345 **When fitting full and history-conditioned psychometric curves to the IBL data21,**

346 **we observed that internal mode processing was associated with a history-**

347 **dependent increase in bias and lapse as well as a history-independent increase**

348 **in threshold (Supplemental Section 1.3.2 and Supplemental Figure S7). Over**

349 **time, the frequency of history-congruent choices increased alongside stimulus-**

350 **congruence and speed of response as mice were exposed to the experiment,**

351 **arguing against the proposition that biases toward perceptual history reflected**

352 **an unspecific response strategy in mice who were not sufficiently trained on the**

353 **IBL task (Supplemental Section 1.4.2 and Supplemental Figure S8)**.

354 **In sum, these analyses confirmed that the observed fluctuations in sensitivity**

355 **to external sensory information are driven by dynamic changes in impact of**

356 **perceptual history and cannot be reduced to general response bias and random**

357 **choice behavior.**

## 358 5.6 Fluctuations in mode result from coordinated changes in the

359 **impact of external and internal information on perception**

360 The empirical data presented above indicate that, for both humans and mice, perception

361 fluctuates between external and modes, i.e., multi-trial epochs that are characterized by

362 enhanced sensitivity toward either external sensory information or internal predictions

363 generated by perceptual history. Since natural environments typically show high temporal

364 redundancy34, previous experiences are often good predictors of new stimuli30,31,35,41. Serial

365 dependencies may therefore induce autocorrelations in perception by serving as internal

366 predictions (or *memory* processes9,13) that actively integrate noisy sensory information over

367 time50.

368 Previous work has shown that such internal predictions can be built by dynamically updating

369 the estimated probability of being in a particular perceptual state from the sequence of

370 preceding experiences35,46,51. The integration of sequential inputs may lead to accumulating

371 effects of perceptual history that progressively override incoming sensory information, enabling

372 internal mode processing19. However, since such a process would lead to internal biases that

373 may eventually become impossible to overcome52, **changes in mode may require** ongoing

374 wave-like fluctuations9,13 in the perceptual impact of external and internal information that

375 occur *irrespective* of the sequence of previous experiences and temporarily de-couple the

376 decision variable from implicit internal representations of the environment19.

377 Following Bayes’ theorem, binary perceptual decisions depend on the log posterior ratio *L* of

378 the two alternative states of the environment that participants learn about via noisy sensory

379 information51. We computed the posterior by combining the sensory evidence available at

380 time-point *t* (i.e., the log likelihood ratio *LLR*) with the prior probability *ψ*, **weighted by**

381 **the respective precision terms** *ωLLR* **and** *ωψ*:

*Lt* = *LLRt ∗ ωLLR* + *ψt*(*Lt−*1*, H*) *∗ ωψ* (1)

382 We derived the prior probability *ψ* at timepoint *t* from the posterior probability of perceptual

383 outcomes at timepoint *Lt−*1. Since a switch between the two states can occur at any time,

384 the effect of perceptual history varies according to both the sequence of preceding experiences

385 and the estimated stability of the external environment (i.e., the *hazard rate H*51):

*ψt*(*Lt−*1*, H*) = *Lt−*1 + *log*(

1 *− H H*

+ *exp*(*−Lt−*1)) *− log*(

1 *− H H*

+ *exp*(*Lt−*1)) (2)

386 The *LLR* was computed from inputs *st* by applying a sigmoid function defined by parameter

387 *α* that controls the sensitivity of perception to the available sensory information (see Methods

388 for details on *st* in humans and mice):

1

= 1 + *exp*(*−α ∗ s* ) (3)

*ut*

*t*

*LLR* = *log*( *ut*

*t* 1

*− ut*

) (4)

389 **To allow for bimodal inference, i.e., alternating periods of internally- and**

390 **externally-biased modes of perceptual processing that occur irrespective of the**

391 **sequence of preceding experiences, we assumed that likelihood and prior vary**

392 **in their influence on the perceptual decision according to fluctuations governed**

393 **by** *ωLLR* **and** *ωψ***. These anti-phase sine functions (defined by amplitudes** *aLLR/ψ***,**

394 **frequency** *f* **and phase** *p***) determine the precision afforded to the likelihood and**

395 **prior53. The implicit anti-phase fluctuations are mandated by Bayes-optimal**

396 **formulations in which inference depends only on the relative values of prior and**

397 **likelihood precision (i.e., the Kalman gain54). As such,** *ωLLR* **and** *ωψ* **implement a**

398 **hyperprior55 in which the likelihood and prior precisions are shifted against each**

399 **other at a dominant timescale defined by** *f* :

*ωLLR* = *aLLR ∗ sin*(*f ∗ t* + *p*) + 1 (5)

*ωψ* = *aψ ∗ sin*(*f ∗ t* + *p* + *π*) + 1 (6)

400 Finally, a sigmoid transform of the posterior *Lt* yields the probability of observing the

401 perceptual decision *yt* at a temperature determined by *ζ−*1:

402

403

404

1

*P yt − P yt*

( = 1) = 1 ( = 0) = 1 + *exp*(*−ζ ∗ L* ) (7)

*t*

**We used a maximum likelihood procedure to fit the bimodal inference model (M1, Figure 1F) to the behavioral data from the Confidence database20 and the IBL database21, optimizing the parameters** *α***,** *H***,** *ampLLR***,** *ampψ***,** *f* **,** *p* **and** *ζ* **(see**

405 **Methods for details and Supplemental Table T2 for a summary of the parameters**

406 **of the bimodal inference model). We validated our model in three steps:**

407 **First, to show that bimodal inference does not emerge spontaneously in normative**

408 **Bayesian models of evidence accumulation, but requires the ad-hoc addition of**

409 **anti-phase oscillations in prior and likelihood precision, we compared the bimodal**

410 **inference model to four control models (M2-5, Figure 1G). In these models, we**

411 **successively removed the anti-phase oscillations (M2-M4) and the integration of**

412 **information across trials (M5) from the bimodal inference model and performed**

413 **a model comparison based on AIC.**

414 **Model M2 (***AIC*2 **=** 9*.*76 *×* 104 **in humans and** 4*.*91 *×* 104 **in mice) and Model M3**

415 **(***AIC*3 **=** 1*.*19 *×* 105 **in humans and** 5*.*95 *×* 104 **in mice) incorporated only oscillations**

416 **of either likelihood or prior precision. Model M4 (***AIC*4 **=** 1*.*69 *×* 105 **in humans**

417 **and** 9*.*12 *×* 104 **in mice) lacked any oscillations of likelihood and prior precision**

418 **and corresponded to the normative model proposed by Glaze et al.51. In model**

419 **M5 (***AIC*4 **=** 2*.*01 *×* 105 **in humans and** 1*.*13 *×* 105 **in mice), we furthermore removed**

420 **the integration of information across trials, such that perception depended only**

421 **in incoming sensory information (Figure 1G).**

422 **The bimodal inference model achieved the lowest AIC across the full model space**

423 **(***AIC*1 **=** 8*.*16 *×* 104 **in humans and** 4*.*24 *×* 104 **in mice) and was clearly superior to**

424 **the normative Bayesian model of evidence accumulation (***δAIC* **=** *−*8*.*79 *×* 104 **in**

425 **humans and** *−*4*.*87 *×* 104 **in mice; Supplemental Figure S9).**

426 **As a second validation of the bimodal inference model, we tested whether the**

427 **posterior model predicted within-training and out-of-training variables. The**

428 **bimodal inference model characterizes each subject by a sensitivity parameter**

429 *α* **(humans:** *α* **=** 0*.*5 ± 1*.*12 *×* 10*−*4**; mice:** *α* **=** 1*.*06 ± 2*.*88 *×* 10*−*3**) that captures**

430 **how strongly perception is driven by the available sensory information, and a**

431 **hazard rate parameter** *H* **(humans:** *H* **=** 0*.*45 ± 4*.*8 *×* 10*−*5**; mice:** *H* **=** 0*.*46 ±

432 2*.*97 *×* 10*−*4**) that controls how heavily perception is biased by perceptual history.**

433 **The parameter** *f* **captures the dominant time scale at which likelihood (amplitude**

434 **humans:** *aLLR* **=** 0*.*5 ± 2*.*02 *×* 10*−*4**; mice:** *aLLR* **=** 0*.*39 ± 1*.*08 *×* 10*−*3**) and prior**

435 **precision (amplitude humans:** *aψ* **=** 1*.*44 ± 5*.*27 *×* 10*−*4**; mice:** *aψ* **=** 1*.*71 ± 7*.*15 *×* 10*−*3**)**

436 **fluctuated and was estimated at** 0*.*11 ± 1*.*68 *×* 10*−*5 **1/***Ntrials* **and** 0*.*11 ± 1*.*63 *×* 10*−*4

437 **1/***Ntrials* **in mice.**

438 As a sanity check for model fit, we tested whether the frequency of stimulus- and history-

439 congruent trials in the Confidence database20 and IBL database21 correlated with the estimated

440 parameters *α* and *H*, respectively. As expected, the estimated sensitivity toward stimulus

441 information *α* was positively correlated with the frequency of stimulus-congruent perceptual

442 choices (humans: *β* = 8*.*4 ± 0*.*26, T(4*.*31 *×* 103) = 32*.*87, p = 1*.*3 *×* 10*−*211; mice: *β* = 1*.*93

443 ± 0*.*12, T(2*.*07 *×* 103) = 16*.*21, p = 9*.*37 *×* 10*−*56). Likewise, *H* was negatively correlated

444 with the frequency of history-congruent perceptual choices (humans: *β* = *−*11*.*84 ± 0*.*5,

445 T(4*.*29 *×* 103) = *−*23*.*5, p = 5*.*16 *×* 10*−*115; mice: *β* = *−*6*.*18 ± 0*.*66, T(2*.*08 *×* 103) = *−*9*.*37,

446 p = 1*.*85 *×* 10*−*20).

447 Our behavioral analyses reveal that humans and mice show significant effects of perceptual

448 history that impaired performance in randomized psychophysical experiments24,28,30,31,43

449 (Figure 2A and 3A). We therefore expected that humans and mice underestimated the true

450

hazard rate *H*ˆ

of the experimental environments (Confidence database20:

*H*ˆ*Humans* = 0*.*5

451

± 1*.*58 *×* 10*−*5); IBL database21:

*H*ˆ*M ice* = 0*.*49 ± 6*.*47 *×* 10*−*5). Indeed, when fitting the

452 bimodal inference model to the trial-wise perceptual choices, we found that the estimated (i.e.,

453

subjective) hazard rate *H* was lower than *H*ˆ

for both humans (*β* = *−*6*.*87 ± 0*.*94, T(61*.*87) =

454 *−*7*.*33, p = 5*.*76 *×* 10*−*10) and mice (*β* = *−*2*.*91 ± 0*.*34, T(112*.*57) = *−*8*.*51, p = 8*.*65 *×* 10*−*14).

455 To further probe the validity of the bimodal inference model, we asked whether posterior

456 model quantities could explain aspects of the behavioral data that the model was not fitted

457 to. We predicted that the posterior decision variable *Lt* not only encodes perceptual choices

458 (i.e., the variable used for model estimation), but also predicts the speed of response and

459 subjective confidence30,44. Indeed, the estimated trial-wise posterior decision certainty *|Lt|*

460 correlated negatively with RTs in humans (*β* = *−*4*.*36 *×* 10*−*3 ± 4*.*64 *×* 10*−*4, T(1*.*98 *×* 106)

461 = *−*9*.*41, p = 5*.*19 *×* 10*−*21) and TDs mice (*β* = *−*35*.*45 ± 0*.*86, T(1*.*28 *×* 106) = *−*41*.*13, p

462 < 2*.*2 *×* 10*−*308). Likewise, subjective confidence reports were positively correlated with the

463 estimated posterior decision certainty in humans (*β* = 7*.*63 *×* 10*−*3 ± 8*.*32 *×* 10*−*4, T(2*.*06 *×* 106)

464 = 9*.*18, p = 4*.*48 *×* 10*−*20).

465 **The dynamic accumulation of information inherent to our model entails that biases**

466 **toward perceptual history are stronger when the posterior decision certainty**

467 **at the preceding trial is high30,31,51. Due to the link between posterior decision**

468 **certainty and confidence, confident perceptual choices should be more likely to**

469 **induce history-congruent perception at the subsequent trial30,31. In line with our**

470 **prediction, logistic regression indicated that history-congruence was predicted**

471 **by the posterior decision certainty** *|Lt−*1*|* **extracted from the model** (humans: *β* =

472 8*.*22 *×* 10*−*3 ± 1*.*94 *×* 10*−*3, z = 4*.*25, p = 2*.*17 *×* 10*−*5; mice: *β* = *−*3*.*72 *×* 10*−*3 ± 1*.*83 *×* 10*−*3,

473 z = *−*2*.*03, p = 0*.*04) and the subjective confidence reported by the participants (humans: *β*

474 = 0*.*04 ± 1*.*62 *×* 10*−*3, z = 27*.*21, p = 4*.*56 *×* 10*−*163) at the preceding trial.

475 **As a third validation of the bimodal inference model, we used the posterior**

476 **model parameters to simulate synthetic perceptual choices and repeated the**

477 **behavioral analyses conducted for the empirical data.** Simulations from the bimodal

478 inference model closely replicated our empirical results: Simulated perceptual decisions

479 resulted from a competition of perceptual history with incoming sensory signals (Figure 4A).

480 Stimulus- and history-congruence were significantly autocorrelated (Figure 4B-C), fluctuating

481 in anti-phase as a scale-invariant process with a 1/f power law (Figure 4D-F). Simulated

482 posterior certainty28,30,44 (i.e., the absolute of the log posterior ratio *|Lt|*) showed a quadratic

483 relationship to the mode of sensory processing (Figure 4H), mirroring the relation of RTs

484 and confidence reports to external and internal biases in perception (Figure 2G-H and Figure

485 3G-H). Crucially, the overlap between empirical and simulated data broke down when we

486 removed the anti-phase oscillations or the accumulation of evidence over time from the

487 bimodal inference model (Supplemental Figures S10-13).

488 **In sum, computational modeling suggested that between-mode fluctuations are**

489 **best explained by two interlinked processes (Figure 1E and F): (i), the dynamic**

490 **accumulation of information across successive trials mandated by normative**

491 **Bayesian models of evidence accumulation and, (ii), ongoing anti-phase oscillations**

492 **in the impact of external and internal information.**

493 **6 Discussion**

494 This work investigates the behavioral and computational characteristics of ongoing fluctuations

495 in perceptual decision-making using two large-scale datasets in humans20 and mice21. We

496 found that humans and mice cycle through recurring intervals of reduced sensitivity to

497 external sensory information, during which they rely more strongly on perceptual history, i.e.,

498 an internal prediction that is provided by the sequence of preceding choices. Computational

499 modeling indicated that these slow periodicities are governed by two interlinked factors: (i),

500 the dynamic integration of sensory inputs over time and, (ii), anti-phase oscillations in the

501 strength at which perception is driven by internal versus external sources of information.

502 These cross-species results suggest that ongoing fluctuations in perceptual decision-making

503 arise not merely as a noise-related epiphenomenon of limited processing capacity, but result

504 from a structured and adaptive mechanism that fluctuates between internally- and externally-

505 oriented modes of sensory analysis.

## 506 6.1 Bimodal inference represents a pervasive aspect of perceptual

507 **decision-making in humans and mice**

508 A growing body of literature has highlighted that perception is modulated by preceding

509 choices22–28,30,32,33. Our work provides converging cross-species evidence supporting the

510 notion that such serial dependencies are a pervasive and general phenomenon of perceptual

511 decision-making (Figures 2 and 3). While introducing errors in randomized psychophysical

512 designs24,28,30,31,43 (Figures 2A and 3A), we found that perceptual history facilitates post-

513 perceptual processes such as speed of response42 (Figure 2G and 3G) and subjective confidence

514 in humans (Figure 2I).

515 At the level of individual traits, increased biases toward preceding choices were associated

516 with reduced sensitivity to external information (Supplemental Figure 1C-D) and lower

517 metacognitive efficiency. When investigating how serial dependencies evolve over time, we

518 observed dynamic changes in the strength of perceptual history (Figures 2 and 3B) that

519 created wavering biases toward internally- and externally-biased modes of sensory processing.

520 Between-mode fluctuations may thus provide a new explanation for ongoing changes in

521 perceptual performance6–11.

522 In computational terms, serial dependencies may leverage the temporal autocorrelation of

523 natural environments31,46 to increase the efficiency of decision-making35,43. Such temporal

524 smoothing46 of sensory inputs may be achieved by updating dynamic predictions about the

525 world based on the sequence of noisy perceptual experiences22,31, **using algorithms based**

526 **on sequential Bayes25,42,51 such as Kalman35 or Hierarchical Gaussian filtering54**.

527 At the level of neural mechanisms, the integration of internal with external information may

528 be realized by combining feedback from higher levels in the cortical hierarchy with incoming

529 sensory signals that are fed forward from lower levels56.

530 Yet relying too strongly on serial dependencies may come at a cost: When accumulating over

531 time, internal predictions may eventually override external information, leading to circular

532 and false inferences about the state of the environment57. Akin to the wake-sleep-algorithm

533 in machine learning58, bimodal inference may help to determine whether errors result from

534 external input or from internally-stored predictions: During internal mode, sensory processing

535 is more strongly constrained by predictive processes that auto-encode the agent’s environment.

536 Conversely, during external mode, the network is driven predominantly by sensory inputs18.

537 Between-mode fluctuations may thus generate an unambiguous error signal that aligns internal

538 predictions with the current state of the environment in iterative test-update-cycles58. On a

539 broader scale, between-mode fluctuations may thus regulate the balance between feedforward

540 versus feedback contributions to perception and thereby play a adaptive role in metacognition

541 and reality monitoring59.

542 **We hypothesized that observers have certain hyperpriors that are apt for ac-**

543 **commodating fluctuations in the predictability of their environment, i.e., people**

544 **believe that their world is inherently volatile. To be Bayes optimal, it is therefore**

545 **necessary to periodically re-evaluate posterior beliefs about the parameters that**

546 **define an internal generative model of the external sensory environment. One**

547 **way to do this is to periodically suspend the precision of prior beliefs and increase**

548 **the precision afforded to sensory evidence, thus updating Bayesian beliefs about**

549 **model parameters.**

550 **The empirical evidence above suggests that the timescale of this periodic schedul-**

551 **ing of evidence accumulation may be scale-invariant. This means that there**

552 **may exist a timescale of periodic fluctuations in precision over every window**

553 **or length of perceptual decision-making. Bimodal inference predicts perceptual**

554 **decisions under a generative model (based upon a hazard function to model**

555 **serial dependencies between subsequent trials) with periodic fluctuations in the**

556 **precision of sensory evidence relative to prior beliefs at a particular timescale.**

557 **Remarkably, a systematic model comparison based on AIC indicated that a**

558 **model with fluctuating precisions has much greater evidence, relative to a model**

559 **in the absence of fluctuating precisions. This ad-hoc addition of oscillations to a**

560 **normative Bayesian model of evidence accumulation51 allowed us to quantify the**

561 **dominant timescale of periodic fluctuations mode at approximately 0.11 1/***Ntrials*

562 **in humans and mice that is appropriate for these kinds of paradigms.**

## 563 6.2 Bimodal inference versus normative Bayesian evidence accu-

564 **mulation**

565 **Could bimodal inference emerge spontaneously in normative models of perceptual**

566 **decision-making? In predictive processing, the relative precision of prior and**

567 **likelihood determines their integration into the posterior that determines the**

568 **content of perception. At the level of individual trials, the perceptual impact**

569 **of internal predictions generated from perceptual history (prior precision) and**

570 **external sensory information (likelihood precision) are thus necessarily anti-**

571 **correlated. The same holds for mechanistic models of drift diffusion, which**

572 **understand choice history biases as driven by changes in the starting point51**

573 **or the drift rate of evidence accumulation32. Under the former formulation,**

574 **perceptual history is bound to have a stronger influence on perception when less**

575 **weight is given to incoming sensory evidence, assuming that the last choice is**

576 **represented as a starting point bias. The effects of choice history in normative**

577 **Bayesian and mechanistic drift diffusion models can be mapped onto one another**

578 **via the Bayesian formulation of drift diffusion60, where the inverse of likelihood**

579 **precision determines the amount of noise in the accumulation of new evidence,**

580 **and prior precision determines the absolute shift in its starting point60.**

581 **While it is thus clear that the impact of perceptual history and sensory evidence**

582 **are anti-correlated *at each individual trial*, we here introduce anti-phase oscilla-**

583 **tions as an ad-hoc modification to model slow fluctuations in prior and likelihood**

584 **precision that evolve *over many consecutive trials* and are not mandated by**

585 **normative Bayesian or mechanistic drift diffusion models. The bimodal infer-**

586 **ence model provides a reasonable explanation of the linked autocorrelations in**

587 **stimulus- and history-congruence, as evidenced by formal model comparison,**

588 **successful prediction of RTs and confidence as out-of-training variables, and a**

589 **qualitative reproduction of our empirical data from posterior model parameter**

590 **as evidence against over- or under-fitting.**

591 **Of note, similar non-stationarities have been observed in descriptive models that**

592 **assume continuous61 or discrete12 changes in the latent states that modulate**

593 **perceptual decision-making at slow timescales.** A recent computational study62 has

594 used a Hidden Markov model to investigate perceptual decision-making in the IBL database21.

595 In analogy to our findings, the authors observed that mice switch between temporally extended

596 *strategies* that last for more than 100 trials: During *engaged* states, perception was highly

597 sensitive to external sensory information. During *disengaged* states, in turn, choice behavior

598 was prone to errors due to enhanced biases toward one of the two perceptual outcomes62.

599 Despite the conceptual differences to our approach (discrete states in a Hidden Markov

600 model that correspond to switches between distinct decision-making strategies62 vs. gradual

601 changes in mode that emerge from sequential Bayesian inference and ongoing **oscillations**

602 in the impact of external relative to internal information), it is tempting to speculate that

603 engaged/disengaged states and between-mode fluctuations might tap into the same underlying

604 phenomenon.

## 605 6.3 Task engagement and residual motor activation as alternative

606 **explanations for bimodal inference**

607 As a functional explanation for bimodal inference, we propose that perception temporarily

608 disengages from internal predictions to form stable inferences about the statistical properties

609 of the sensory environment. **Between-mode fluctuations may thus elude circular**

610 **inferences that occur when both the causes and the encoding of sensory stimuli**

611 **are volatile19,57.** By the same token, we suggest that fluctuations in mode occur at the

612 level of perceptual processing26,30,46,47, and are not a passive phenomenon that is primarily

613 driven by factors situated up- or downstream of sensory analysis.

614 **How does attention relate to phenomenon of between-mode fluctuations? Ac-**

615 **cording to predictive processing, attention corresponds to the precision afforded**

616 **to the probability distributions that underlie perceptual inference53. From this**

617 **perspective, fluctuations between external and internal mode can be understood**

618 **as ongoing shifts in the attention afforded to either external sensory information**

619 **(regulated via likelihood precision) or internal predictions (regulated via prior**

620 **precision). When the precision of either likelihood or prior increases, posterior**

621 **precision increases, which leads to faster RTs and higher confidence. Therefore,**

622 **when defined from the perspective of predictive processing as the precision af-**

623 **forded to likelihood and prior53, fluctuations in attention may provide a plausible**

624 **explanation for the quadratic relationship of mode to RTs and confidence (Figure**

625 **2H and J; Figure 3I, Figure 4I)**.

626 **Outside of the predictive processing field, attention is often understood in the**

627 **context of task engagement63, which varies according to the availability of cognitive**

628 **resources that are modulated by factors such as tonic arousal, familiarity with**

629 **the task, or fatigue63. Our results suggest that internal mode processing cannot**

630 **be completely reduced to intervals of low task engagement: In addition to shorter**

631 **RTs and elevated confidence, choices during internal mode were not random**

632 **or globally biased, but driven by perceptual history (Supplemental Section).**

633 **Moreover, our computational model identified the dominant timescale of between-**

634 **mode fluctuations at 0.11 1/***Ntrials***, which may be compatible with fluctuations in**

635 **arousal64, but is faster than to be expected for the development of task familiarity**

636 **or fatigue.**

637 **However, in interpreting the impact of between-mode fluctuations on perceptual**

638 **accuracy, speed of response and confidence, it is important to consider that global**

639 **modulators such as tonic arousal are known to have non-linear effects on task**

640 **performance65: In perceptual tasks, performance seems so be highest during**

641 **mid-level arousal, whereas low- and high-level arousal lead to reduced accuracy**

642 **and slower responses65. This contrasts with the effects of bimodal inference,**

643 **where accuracy increases linearly as one moves from internal to external mode,**

644 **and responses become faster at both ends of the mode spectrum.**

645 **Of note, high phasic arousal has been shown to suppress biases in decision-making**

646 **in humans and mice across domains66–68, including biases toward perceptual**

647 **history28 that we implicate in internal mode processing. While the increase in**

648 **response speed and history congruence over time (Supplemental Section 1.4) may**

649 **argue against insufficient training as an alternative explanation for internal mode**

650 **processing, it may also be indicative of waning arousal. The multiple mechanistic**

651 **mappings to RTs and confidence warrant more direct measures of arousal (such**

652 **as pupil size28,65,66,68–70, motor behavior69,70, or neural data71) to better delineate**

653 **bimodal inference from fluctuations in global modulators of task performance.**

654 **Residual activation of the motor system may provide another contribution to**

655 **serial biases in perceptual choices72. Such motor-driven priming may lead to**

656 **errors in randomized psychophysical designs, resembling the phenomenon that**

657 **we identify as internally-biased processing73. Moreover, residual activation of the**

658 **motor system may lead to faster responses, and thus constitutes an alternative**

659 **explanation for the quadratic relationship of mode with RTs72. The observation**

660 **of elevated confidence for stronger biases toward internal mode speaks against**

661 **the proposition that residual activation of the motor system is the primary**

662 **driver of serial choice biases, since strong motor-driven priming should lead to**

663 **frequent lapses that are typically associated reduced confidence74. Likewise,**

664 **perceptual history effects have repeatedly been replicated in experiments with**

665 **counter-balanced stimulus-response mappings30: Feigin2021.**

666 **No-response paradigms, in which perceptual decision are inferred from eye-**

667 **movements alone, could help to better differentiate perceptual from motor-**

668 **related effects. Likewise, video-tracking of response behavior and neural record-**

669 **ing from motor- and premotor, which has recently been released for the IBL**

670 **database[IBL2023], may provide further insight into the relation of motor behavior**

671 **to the perceptual phenomenon of between-mode fluctuations.**

## 672 6.4 Limitations and open questions

673 **Our results suggest bimodal inference as a pervasive aspect of perceptual decision-**

674 **making in humans and mice. However, a number of limitations and open questions**

675 **have to be considered:**

676 **First, this work sought to understand whether fluctuations between internal**

677 **and external mode, which we initially observed in an experiment on bistable**

678 **perception in humans19, represent a general phenomenon that occurs across a**

679 **diverse set of perceptual decision-making tasks. Our analysis of the Confidence**

680 **database20 therefore collapsed across all available experiments on binary percep-**

681 **tual decision-making. Individual experiments differed with respect to the stimuli,**

682 **the manipulation of difficulty, the timing of trials, and the way responses were**

683 **collected, but were highly comparable with respect to the central variables of**

684 **stimulus- and history-congruence (Supplemental Figure S1A-B).**

685 **The variability across experiments, which we considered as random effects in all**

686 **statistical analyses, enabled us to assess whether bimodal inference represents a**

687 **general phenomenon in perceptual decision-making, but limited the precision at**

688 **which we were able to investigate the relation of mode to behavioral variables such**

689 **as timing, task difficulty, RT or confidence. This issue is partially resolved by our**

690 **analyses of the IBL database, which replicated our findings in an experiment that**

691 **was highly standardized with respect to timing, task difficulty, and behavioral**

692 **read-out21. It will be an important task for future research to validate our results**

693 **on bimodal inference in a standardized dataset of comparable volume in humans,**

694 **which is, to our knowledge, not yet available.**

695 **Second, our results point to an attraction of perception toward preceding choices.**

696 **Previous work has shown that perceptual decision-making is concurrently affected**

697 **by both attractive and repulsive serial biases that operate on distinct time-**

698 **scales and serve complementary functions for sensory processing27,75,76: Short-**

699 **term attraction may serve the decoding of noisy sensory inputs and increase**

700 **the stability of perception, whereas long-term repulsion may enable efficient**

701 **encoding and sensitivity to change27. In the data analyzed here, history biases**

702 **tended to be repetitive (Figure 2A, Figure 3A, Supplemental Figure S6 and**

703 **S7), and only 2 of the 66 experiments of the Confidence database20 showed**

704 **significant alternating biases (Supplemental Figure S1). However, as we show in**

705 **Supplemental Figure S14, fluctuations in both alternating and repeating history**

706 **biases generate overlapping autocorrelation curves. Our analysis of between-**

707 **mode fluctuations is therefore not tied exclusively to repeating biases, but**

708 **accommodates alternating biases as well, such that both may lead to internally-**

709 **biased processing and reduced sensitivity to external sensory information. Future**

710 **work could apply our approach to paradigms that boost alternating as opposed**

711 **to repeating biases, as this would help to better understand how repetition**

712 **and alternation are linked in terms of their computational function and neural**

713 **implementation27.**

714 **A third open question concerns the computational underpinnings of bimodal**

715 **inference. The addition of slow anti-phase oscillations to the integration of prior**

716 **and likelihood represents an ad-hoc modification of a normative Bayesian model**

717 **of evidence accumulation51. While the bimodal inference model is supported by**

718 **formal model comparison, the successful prediction of out-of-training variables**

719 **and the qualitative reproduction of our empirical data in simulations from pos-**

720 **terior model parameters, it is an important task for future research to test (i),**

721 **whether between-mode fluctuations can emerge spontaneously in hierarchical**

722 **models of Bayesian inference, (ii), whether modes are continuous19 or discrete62,**

723 **and (iii), whether bimodal inference can be causally manipulated by experi-**

724 **mental variables. We speculate that between-mode fluctuations may separate**

725 **the perceptual contribution of internal predictions and external sensory data**

726 **in time, creating unambiguous learning signals that benefit inference about the**

727 **precision of prior and likelihood, respectively. This proposition should be tested**

728 **empirically by relating the phenomenon of bimodal inference to performance in,**

729 **e.g., reversal learning, probabilistic reasoning, or metacognition.**

730 **A final important avenue for further research on bimodal inference is to elucidate**

731 **its neurobiological underpinnings.** Since between-mode fluctuations were found in

732 humans and mice, future studies can apply non-invasive and invasive neuro-imaging and

733 electrophysiology to better understand the neural mechanisms that generate ongoing changes

734 in mode in terms of their neuro-anatomy, -chemistry and -circuitry.

735 Establishing the neural correlates of externally- an internally-biased modes will enable exiting

736 opportunities to investigate their role for adaptive perception and decision-making: Causal

737 interventions via pharmacological challenges, optogenetic manipulations or (non-)invasive

738 brain stimulation will help to understand whether between-mode fluctuations are implicated

739 in resolving credit-assignment problems18,77 or in calibrating metacognition and reality

740 monitoring59. Answers to these questions may provide new insights into the pathophysiology

741 of hallucinations and delusions, which have been characterized by an imbalance in the impact

742 of external versus internal information56,78,79 and are typically associated with metacognitive

743 failures and a departure from consensual reality79.

744 **7 Methods**

## 745 7.1 Resource availability

746 **7.1.1 Lead contact**

747 Further information and requests for resources should be directed to and will be fulfilled by

748 the lead contact, Veith Weilnhammer (v[eith.weilnhammer@gmail.com](mailto:veith.weilnhammer@gmail.com)).

749 **7.1.2 Materials availability**

750 This study did not generate new unique reagents.

751 **7.1.3 Data and code availability**

752 All custom code and behavioral data are available on [https://github.com/veithweilnhammer/](https://github.com/veithweilnhammer/Modes)

753 [Modes.](https://github.com/veithweilnhammer/Modes) This manuscript was created using the *R Markdown* framework, which integrates all

754 data-related computations and the formatted text within one document. With this, we wish

755 to make our approach fully transparent and reproducible for reviewers and future readers.

## 756 7.2 Experimental model and subject details

757 **7.2.1 Confidence database**

758 **We downloaded the human data from the Confidence database20 on 10/21/2020,**

759 **limiting our analyses to the category *perception*. Within this category, we**

760 **selected studies in which participants made binary perceptual decisions between**

761 **two alternatives. We excluded two experiments in which the average perceptual**

762 **accuracy fell below 50%. After excluding these experiments, our sample consisted**

763 **of** 21*.*05 **million trials obtained from 4317 human participants and 66 individual**

764 **experiments (Supplemental Table 1). Out of the 66 included experiments, 62**

765 **investigated visual, 1 auditory, 2 proprioceptive, and 1 multimodal perception.**

766 **59 experiments were based on discrimination and 6 on detection, with one**

767 **investigating both.**

768 **7.2.2 IBL database**

769 We downloaded the data from the IBL database21 on 04/28/2021. We limited our analyses to

770 the *basic task*, during which mice responded to gratings that appeared with equal probability

771 in the left or right hemifield. Within each mouse, we excluded sessions in which perceptual

772 accuracy was below 80% for stimuli presented at a contrast *≥* 50%. After exclusion, our

773 sample consisted of 1*.*46 million trials trials obtained from N = 165 mice.

## 774 7.3 Method details

775 **7.3.1 Variables of interest**

776 **Primary variables of interest:** We extracted trial-wise data on the presented stimulus and

777 the associated perceptual decision. Stimulus-congruent choices were defined by perceptual

778 decisions that matched the presented stimuli. History-congruent choices were defined by

779 perceptual choices that matched the perceptual choice at the immediately preceding trial.

780 The dynamic probabilities of stimulus- and history-congruence were computed in sliding

781 windows of ±5 trials.

782 The *mode* of sensory processing was derived by subtracting the dynamic probability of history-

783 congruence from the dynamic probability of stimulus-congruence, such that positive values

784 indicate externally-oriented processing, whereas negative values indicate internally-oriented

785 processing. When visualizing the relation of the mode of sensory processing to confidence,

786 RTs or trial duration (see below), we binned the mode variable in 10% intervals. We excluded

787 bins that contained less than 0.5% of the total number of available data-points.

788 **Secondary variables of interest**: From the Confidence Database20, we furthermore

789 extracted trial-wise confidence reports and RTs. **Out of the 58 experiments that provide**

790 **information on RTs, 46 cued the response by the onset of a response screen or**

791 **an additional response cue, whereas 14 allowed participants to response at any**

792 **time after stimulus onset.** If RTs were available for both the perceptual decision and

793 the confidence report, we only extracted the RT associated with the perceptual decision.

794 To enable comparability between studies, we normalized RTs and confidence reports within

795 individual studies using the *scale* R function. If not available for a particular study, RTs were

796 treated as missing variables. From the IBL database21, we extracted trial durations (TDs) as

797 defined by interval between stimulus onset and feedback, which represents a coarse measure

798 of RT21.

799 **Exclusion criteria for individual data-points:** For non-normalized data (TDs from

800 the IBL database21; d-prime, meta-dprime and M-ratio from the Confidence database20 and

801 simulated confidence reports), we excluded data-points that differed from the median by

802 more than 3 x MAD (median absolute distance49). For normalized data (RTs and confidence

803 reports from the Confidence database20), we excluded data-points that differed from the

804 mean by more than 3 x SD (standard deviation).

805 **7.3.2 Control variables**

806 Next to the sequence of presented stimuli, we assessed the autocorrelation of task difficulty

807 as an alternative explanation for any autocorrelation in stimulus- and history-congruence. In

808 the Confidence Database20, **21 of the 66 included experiments used fixed difficulty**

809 **levels, whereas 45 manipulated difficulty levels within participants. Difficulty**

810 **was manipulated via noise masks, contrast, luminance, presentation time, or**

811 **stimulus probability for gabors, dot coherence for random dot kinematograms,**

812 **difference in elements and set size for comparisons of numerosity, difference in**

813 **clicks for auditory discrimination, temporal distance for meta-contrast masking,**

814 **and amount of self-motion for proprioception. We treated task difficulty as a**

815 **missing variable for the experiments that fixed it at the participant-level, as**

816 **this precluded the computation of autocorrelation curves.** In analogy to RTs and

817 confidence, difficulty levels were normalized within individual studies. For the IBL Database21,

818 task difficulty was defined by the contrast of the presented grating.

819 **7.3.3 Autocorrelations**

820 For each participant, trial-wise autocorrelation coefficients were estimated using the R-function

821 *acf* with a maximum lag defined by the number of trials available per subject. Autocorrelation

822 coefficients are displayed against the lag (in numbers of trials, ranging from 1 to 20) relative to

823 the index trial (t = 0; Figure 2B-C, 3B-C and 4B-C). To account for spurious autocorrelations

824 that occur due to imbalances in the analyzed variables, we estimated autocorrelations for

825 randomly permuted data (100 iterations). For group-level autocorrelations, we computed

826 the differences between the true autocorrelation coefficients and the mean autocorrelation

827 observed for randomly permuted data and averaged across participants.

828 At a given trial, group-level autocorrelation coefficients were considered significant when

829 linear mixed effects modeling indicated that the difference between real and permuted

830 autocorrelation coefficients was above zero at an alpha level of 0.05%. To test whether the

831 autocorrelation of stimulus- and history-congruence remained significant when controlling for

832 task difficulty and the sequence of presented stimuli, we added the respective autocorrelation

833 as an additional factor to the linear mixed effects model that computed the group-level

834 statistics (see also *Mixed effects modeling*).

835 To assess autocorrelations at the level of individual participants, we counted the number of

836 subsequent trials (starting at the first trial after the index trial) for which less than 50% of

837 the permuted autocorrelation coefficients exceeded the true autocorrelation coefficient. For

838 example, a count of zero indicates that the true autocorrelation coefficients exceeded *less*

839 *than 50%* of the autocorrelation coefficients computed for randomly permuted data at the

840 first trial following the index trial. A count of five indicates that, for the first five trials

841 following the index trial, the true autocorrelation coefficients exceeded *more than 50%* of

842 the respective autocorrelation coefficients for the randomly permuted data; at the 6th trial

843 following the index trial, however, *less than 50%* of the autocorrelation coefficients exceeded

844 the respective permuted autocorrelation coefficients.

845 **7.3.4 Spectral analysis**

846 We used the R function *spectrum* to compute the spectral densities for the dynamic probabil-

847 ities of stimulus- and history-congruence as well as the phase (i.e., frequency-specific shift

848 between the two time-series ranging from 0 to 2 *∗π*) and squared coherence (frequency-specific

849 variable that denotes the degree to which the shift between the two time-series in constant,

850 ranging from 0 to 100%). Periodograms were smoothed using modified Daniell smoothers at

851 a width of 50.

852 Since the dynamic probabilities of history- and stimulus-congruence were computed using

853 a sliding windows of ±5 trials (i.e., intervals containing a total of 11 trials), we report the

854 spectral density, coherence and phase for frequencies below 1/11 1/*Ntrials*. Spectral densities

855 have one value per subject and frequency (data shown in Figures 2D and 3D). To assess the

856 relation between stimulus- and history-congruence in this frequency range, we report average

857 phase and average squared coherence for all frequencies below 1/11 1/*Ntrials* (i.e., one value

858 per subject; data shown in Figure 2E-F and 3E-F).

859 Since the data extracted from the Confidence Database20 consist of a large set of individual

860 studies that differ with respect to inter-trial intervals, we defined the variable *frequency* in

861 the dimension of cycles per trial 1/*Ntrials* rather than cycles per second (Hz). For consistency,

862 we chose 1/*Ntrials* as the unit of frequency for the IBL database21 as well.

## 863 7.4 Quantification and statistical procedures

864 All aggregate data are reported and displayed with errorbars as mean ± standard error of

865 the mean.

866 **7.4.1 Mixed effects modeling**

867 Unless indicated otherwise, we performed group-level inference using the R-packages *lmer*

868 and *afex* for linear mixed effects modeling and *glmer* with a binomial link-function for logistic

869 regression. We compared models based on AIC. To account for variability between the studies

870 available from the Confidence Database20, mixed modeling was conducted using random

871 intercepts defined for each study. To account for variability across experimental session within

872 the IBL database21, mixed modeling was conducted using random intercepts defined for each

873 individual session. When multiple within-participant datapoints were analyzed, we estimated

874 random intercepts for each participant that were *nested* within the respective study of the

875 Confidence database20. By analogy, for the IBL database21, we estimated random intercepts

876 for each session that were nested within the respective mouse. We report *β* values referring

877 to the estimates provided by mixed effects modeling, followed by the respective T statistic

878 (linear models) or z statistic (logistic models).

879 The effects of stimulus- and history-congruence on RTs and confidence reports (Figure 2, 3

880 and 4, subpanels G-I) were assessed in linear mixed effects models that tested for main effects

881 of both stimulus- and history-congruence as well as the between-factor interaction. Thus, the

882 significance of any effect of history-congruence on RTs and confidence reports was assessed

883 while controlling for the respective effect of stimulus-congruence (and vice versa).

884 **7.4.2 Psychometric function**

885 We obtained psychometric curves by fitting the following error function to the behavioral

886 data:

*yp* = *γ* + (1 *− γ − δ*) *∗* (*erf* (

*sw* + *µ t*

) + 1)*/*2 (8)

887 We used the Broyden–Fletcher–Goldfarb–Shanno algorithm in maximum likelihood

888 estimation80 to predict individual choices *y* (outcome A: *y* = 0; outcome B: *y* = 1) from the

889 choice probability *yp*. In humans, we computed *sw* by multiplying the inputs *s* (stimulus A:

890 0; outcome B: 1) with the task difficulty *Db* (binarized across 7 levels):

*sw* = (*s −* 0*.*5) *∗ Db* (9)

891 In mice, *sw* was defined by the respective stimulus contrast in the two hemifields:

*sw* = *ContrastRight − ContrastLeft* (10)

892 Parameters of the psychometric error function were fitted using the R-package *optimx*80. The

893 psychometric error function was defined via the parameters *γ* (lower lapse; lower bound = 0,

894 upper bound = 0.5), *δ* (upper lapse; lower bound = 0, upper bound = 0.5), *µ* (bias; lower

895 bound humans = -5; upper bound humans = 5, lower bound mice = -0.5, upper bound mice

896 = 0.5) and threshold *t* (lower bound humans = 0.5, upper bound humans = 25; lower bound

897 mice = 0.01, upper bound mice = 1.5).

898 **7.4.3 Computational modeling**

899 **Model definition**: Our modeling analysis is an extension of a model proposed by Glaze et

900 al.51, who defined a normative account of evidence accumulation for decision-making. In this

901 model, trial-wise choices are explained by applying Bayes theorem to infer moment-by-moment

902 changes in the state of environment from trial-wise noisy observations across trials.

903 Following Glaze et al.51, we applied Bayes rule to compute the posterior evidence for the

904 two alternative choices (i.e., the log posterior ratio *L*) from the sensory evidence available at

905 time-point *t* (i.e., the log likelihood ratio *LLR*) with the prior probability *ψ*, **weighted by**

906 **the respective precision terms** *ωLLR* **and** *ωψ*:

*Lt* = *LLRt ∗ ωLLR* + *ψt*(*Lt−*1*, H*) *∗ ωψ* (11)

907 In the trial-wise design studied here, a transition between the two states of the environment

908 (i.e., the sources generating the noisy observations available to the participant) can occur

909 at any time. Despite the random nature of the psychophysical paradigms studied here20,21,

910 humans and mice showed significant biases toward preceding choices (Figure 2A and 3A).

911 We thus assumed that the prior probability of the two possible outcomes depends on the

912 posterior choice probability at the preceding trial and the hazard rate *H* assumed by the

913 participant. Following Glaze et al.51, the prior *ψ* is thus computed as follows:

*ψt*(*Lt−*1*, H*) = *Lt−*1 + *log*(

1 *− H H*

+ *exp*(*−Lt−*1)) *− log*(

1 *− H H*

+ *exp*(*Lt−*1)) (12)

914 In this model, humans, mice and simulated agents make perceptual choices based on noisy

915 observations *u*. The are computed by applying a sensitivity parameter *α* to the content of

916 external sensory information *s*. For humans, we defined the input *s* by the two alternative

917 states of the environment (stimulus A: *s* = 0; stimulus B: *s* = 1), which generated the

918 observations *u* through a sigmoid function that applied a sensitivity parameter *α*:

*ut* = 1 + *exp*(*−α ∗* (*s*

1

*t*

*−* 0*.*5))

919 In mice, the inputs *s* were defined by the respective stimulus contrast in the two hemifields:

(13)

*st* = *ContrastRight − ContrastLeft* (14)

920 As in humans, we derived the input *u* by applying a sigmoid function with a sensitivity

921 parameter *α* to input *s*:

1

= 1 + *exp*(*−α ∗ s* ) (15)

*ut*

*t*

922 For humans, mice and in simulations, the log likelihood ratio *LLR* was computed from *u* as

923 follows:

*LLR* = *log*( *ut*

*t* 1

*− ut*

) (16)

924 To allow for long-range autocorrelation in stimulus- and history-congruence (Figure 2B and

925 3B), our modeling approach differed from Glaze et al.51 in that it allowed for systematic

926 fluctuation in the impact of sensory information (i.e., *LLR*) and the prior probability

927 of choices *ψ* on the posterior probability *L*. This was achieved by multiplying the log

928 likelihood ratio and the log prior ratio with coherent anti-phase fluctuations according to

929 *ωLLR* = *aLLR ∗ sin*(*f ∗ t* + *phase*) + 1 and *ωψ* = *aψ ∗ sin*(*f ∗ t* + *phase* + *π*) + 1.

930 **Model fitting**: In model fitting, we predicted the trial-wise choices *yt* (option A: 0; option B:

931 1) from inputs *s*. To this end, we minimized the log loss between *yt* and the choice probability

932 *ypt* in the unit interval. *ypt* was derived from *Lt* using a sigmoid function defined by the

933 inverse decision temperature *ζ*:

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942

1

*ypt*

= 1 + *exp*(*−ζ ∗ L* ) (17)

*t*

This allowed us to infer the free parameters *H* (lower bound = 0, upper bound = 1; human posterior = 0*.*45 ± 4*.*8 *×* 10*−*5; mouse posterior = 0*.*46 ± 2*.*97 *×* 10*−*4), *α* (lower bound

= 0, upper bound = 5; human posterior = 0*.*5 ± 1*.*12 *×* 10*−*4; mouse posterior = 1*.*06 ±

2*.*88 *×* 10*−*3), *aψ* (lower bound = 0, upper bound = 10; human posterior = 1*.*44 ± 5*.*27 *×* 10*−*4; mouse posterior = 1*.*71 ± 7*.*15 *×* 10*−*3), *ampLLR* (lower bound = 0, upper bound = 10; human posterior = 0*.*5 ± 2*.*02 *×* 10*−*4; mouse posterior = 0*.*39 ± 1*.*08 *×* 10*−*3), frequency *f* (lower bound = 1/40, upper bound = 1/5; human posterior = 0*.*11 ± 1*.*68 *×* 10*−*5; mouse posterior = 0*.*11 ± 1*.*63 *×* 10*−*4), *p* (lower bound = 0, upper bound = 2 *∗ π*; human posterior

= 2*.*72ś4*.*41 *×* 10*−*4; mouse posterior = 2*.*83 ± 3*.*95 *×* 10*−*3) and inverse decision temperature *ζ*

943 (lower bound = 1, upper bound = 10; human posterior = 4*.*63 ± 1*.*95 *×* 10*−*4; mouse posterior

944 = 4*.*82 ± 3*.*03 *×* 10*−*3) using maximum likelihood estimation with the Broyden–Fletcher–

945 Goldfarb–Shanno algorithm as implemented in the R-function *optimx*80 **(see Supplemental**

946 **Table T2 for a description of our model parameters)**.

947 **We validated the bimodal inference model in three steps: a formal model com-**

948 **parison to reduced models based on AIC (Figure 1F-G; Supplemental Figure**

949 **S9), the prediction of within-training (stimulus- and history-congruence) as well**

950 **as out-of-training variables (RT and confidence), and a qualitative reproduction**

951 **of the empirical data from model simulations based on estimated parameters**

952 **(Figure 4).**

953 **Model comparison. We assessed the following model space based on AIC:**

954 • **The full *bimodal inference model* (M1; Figure 1F) incorporates the influ-**

955 **ence of sensory information according to the parameter** *α* **(likelihood); the**

956 **integration of evidence across trials according to the parameter** *H* **(prior);**

957 **anti-phase oscillations in between likelihood and prior precision according**

958 **to** *ωLLR* **and** *ωψ* **with parameters** *aLLR* **(amplitude likelihood fluctuation),** *aψ*

959 **(amplitude prior fluctuation),** *f* **(frequency) and** *p* **(phase).**

960 • **The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the**

961 **influence of sensory information according to parameter** *α* **(likelihood); the**

962 **integration of evidence across trials according to parameter** *H* **(prior); os-**

963 **cillations in likelihood precision according to** *ωLLR* **with parameters** *aLLR*

964 **(amplitude likelihood fluctuation),** *f* **(frequency) and** *p* **(phase).**

965 • **The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence**

966 **of sensory information according to parameter** *α* **(likelihood); the integration**

967 **of evidence across trials according to parameter** *H* **(prior); oscillations in**

968 **the prior precision according to** *ωψ* **with parameters** *aψ* **(amplitude prior**

969 **fluctuation),** *f* **(frequency) and** *p* **(phase). Please note that all models M1-3**

970 **lead to shifts in the relative precision of likelihood and prior.**

971 • **The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the**

972 **influence of sensory information according to parameter** *α* **(likelihood); the**

973 **integration of evidence across trials according to parameter** *H* **(prior), There**

974 **are no additional oscillations. Model M4 thus corresponds to the model**

975 **proposed by Glaze et al. and captures normative evidence accumulation**

976 **in unpredictable environments using a Bayesian update scheme51. The**

977 **comparison against M4 tests the null hypothesis that fluctuations in mode**

978 **emerge from a normative Bayesian model without the ad-hoc addition of**

979 **oscillations as in models M1-3.**

980 • **The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence**

981 **of sensory information according to parameter** *α* **(likelihood). The model**

982 **lacks integration of evidence across trials (flat prior) and oscillations. The**

983 **comparison against M5 tests the null hypothesis that observers do not use**

984 **prior information derived from serial dependency in perception.**

985 **Prediction of within-training and out-of-training variables. To validate our model,**

986 **we correlated individual posterior parameter estimates with the respective con-**

987 **ventional variables. As a sanity check, we tested (i), whether the estimated hazard**

988 **rate** *H* **correlated negatively with the frequency of history-congruent choices**

989 **and, (ii), whether the estimated sensitivity to sensory information** *α* **correlated**

990 **positively with the frequency of stimulus-congruent choices. In addition, we**

991 **tested whether the posterior decision certainty (i.e.. the absolute of the log**

992 **posterior ratio) correlated negatively with RTs and positively with confidence.**

993 **This allowed us to assess whether our model could explain aspects of the data it**

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| 1001 | *ζ***) to define individual parameters for simulation in 4317 simulated participants** |
| 1002 | **(i.e., equivalent to the number of human participants). For each participant, the** |
| 1003 | **number of simulated trials was drawn at random between 300 to 700. Inputs** *s* |
| 1004 | **were drawn at random for each trial, such that the sequence of inputs to the** |
| 1005 | **simulation did not contain any systematic seriality. Noisy observations** *u* **were** |
| 1006 | **generated by applying the posterior parameter** *α* **to inputs** *s***, thus generating** |
| 1007 | **stimulus-congruent choices in** 71*.*36 ± 2*.*6 *×* 10*−*3**% of trials. Choices were simulated** |
| 1008 | **based on the trial-wise choice probabilities** *yp* **obtained from our model. Simulated** |
| 1009 | **data were analyzed in analogy to the human and mouse data. As a substitute of** |
| 1010 | **subjective confidence, we computed the absolute of the trial-wise log posterior** |
| 1011 | **ratio** *|L|* **(i.e., the posterior decision certainty).** |

**was not fitted to (i.e., RTs and confidence).**

**Simulations. Finally, we used simulations (Figure 4, Supplemental Figures S10- 13) to show that all model components, including the anti-phase oscillations governed by** *aψ***,** *aLLR***,** *f* **and** *p***, were necessary for our model to reproduce the characteristics of the empirical data. This enabled us to assess over- or under- fitting in the bimodal inference model and all reduced models M2-M5. We used the posterior model parameters observed for humans (***H***,** *α***,** *aψ***,** *aLLR***,** *f* **,** *p* **and**

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# Figures

## Figure 1

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**Figure 1. Concept.**

|  |  |
| --- | --- |
| 1016 | A. In binary perceptual decision-making, a participant is presented with stimuli from two |
| 1017 | categories (A vs. B; dotted line) and reports consecutive perceptual choices via button presses |
| 1018 | (sold line). All panels below refer to these stimulated example data. |
| 1019 | B. When the response matches the external stimulus information (i.e., overlap between dotted |
| 1020 | and solid line in panel A), perceptual choices are *stimulus-congruent* (red line). When the |
| 1021 | response matches the response at the preceding trial, perceptual choices are *history-congruent* |

|  |  |
| --- | --- |
| 1022 | (blue line). |
| 1023 | C. The dynamic probabilities of stimulus- and history-congruence (i.e., computed in sliding |
| 1024 | windows of ±5 trials) fluctuate over time. |
| 1025 | D. The *mode* of perceptual processing is derived by computing the difference between the |
| 1026 | dynamic probabilities of stimulus- and history-congruence. Values above 0% indicate a |
| 1027 | bias toward external information, whereas values below 0% indicate a bias toward internal |
| 1028 | information. |
| 1029 | E. In computational modeling, internal mode is caused by an enhanced impact of perceptual |
| 1030 | history. This causes the posterior (black line) to be close to the prior (blue line). Conversely, |
| 1031 | during external mode, the posterior is close to the sensory information (log likelihood ratio, |
| 1032 | red line). |
| 1033 | **F. The bimodal inference model (M1) explains fluctuations between externally-** |
| 1034 | **and externally-biased modes (left panel) by two interacting factors: a normative** |
| 1035 | **accumulation of evidence according to parameters** *H* **(middle panel), and anti-** |
| 1036 | **phase oscillations in the precision terms** *ωLLR* **and** *ωψ* **(right panel).** |
| 1037 | **G. The control models M2-M5 were constructed by successively removing the anti-** |
| 1038 | **phase oscillations and the integration of information from the bimodal inference** |
| 1039 | **model. Please note that the normative-evidence-accumulation-model (M4) corre-** |
| 1040 | **sponds to the model proposed by Glaze et al.51. In the no-evidence-accumulation** |
| 1041 | **model (M5), perceptual decisions depend only on likelihood information (flat** |
| 1042 | **priors).** |

1043

## Figure 2

|  |  |
| --- | --- |
| 1045 | **Figure 2. Internal and external modes in human perceptual decision-making.** |
| 1046 | A. In humans, perception was stimulus-congruent in 73.46% ± 0.15% (in red) and history- |
| 1047 | congruent in 52.7% ± 0.12% of trials (in blue; upper panel). History-congruent perceptual |
| 1048 | choices were more frequent when perception was stimulus-incongruent (i.e., on *error* trials; |
| 1049 | lower panel), indicating that history effects impair performance in randomized psychophysical |
| 1050 | designs. |
| 1051 | B. Relative to randomly permuted data, we found highly significant autocorrelations of |
| 1052 | stimulus-congruence and history-congruence (dots indicate intercepts *̸*= 0 in trial-wise linear |
| 1053 | mixed effects modeling at p < 0.05). Across trials, the autocorrelation coefficients were best |
| 1054 | fit by an exponential function (adjusted *R*2 for stimulus-congruence: 0.53; history-congruence: |
| 1055 | 0.72) as compared to a linear function (adjusted *R*2 for stimulus-congruence: 0.53; history- |
| 1056 | congruence: 0.51), decaying at a rate of *γ* = *−*1*.*92 *×* 10*−*3 ± 4*.*5 *×* 10*−*4 (T(6*.*88 *×* 104) |

|  |  |
| --- | --- |
| 1057 | = *−*4*.*27, p = 1*.*98 *×* 10*−*5) for stimulus-congruence and at a rate of *γ* = *−*6*.*11 *×* 10*−*3 ± |
| 1058 | 5*.*69 *×* 10*−*4 (T(6*.*75 *×* 104) = *−*10*.*74, p = 7*.*18 *×* 10*−*27) for history-congruence. |
| 1059 | C. Here, we depict the number of consecutive trials at which autocorrelation coefficients |
| 1060 | exceeded the respective autocorrelation of randomly permuted data within individual partici- |
| 1061 | pants. For stimulus-congruence (upper panel), the lag of positive autocorrelation amounted |
| 1062 | to 3*.*24 ± 2*.*39 *×* 10*−*3 on average, showing a peak at trial t+1 after the index trial. For |
| 1063 | history-congruence (lower panel), the lag of positive autocorrelation amounted to 4*.*87 ± |
| 1064 | 3*.*36 *×* 10*−*3 on average, peaking at trial t+2 after the index trial. |
| 1065 | D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ±5 |
| 1066 | trials) fluctuated as **a scale-invariant process with a 1/f power law**, i.e., at power |
| 1067 | densities that were inversely proportional to the frequency. |
| 1068 | E. The distribution of phase shift between fluctuations in stimulus- and history-congruence |
| 1069 | peaked at half a cycle (*π* denoted by dotted line). |
| 1070 | F. The average squared coherence between fluctuations in stimulus- and history-congruence |
| 1071 | (black dotted line) amounted to 6*.*49 ± 2*.*07 *×* 10*−*3% |
| 1072 | G. We observed faster RTs for both stimulus-congruence (as opposed to stimulus-incongruence, |
| 1073 | *β* = *−*0*.*14 ± 1*.*6 *×* 10*−*3, T(1*.*99 *×* 106) = *−*85*.*84, p < 2*.*2 *×* 10*−*308) and history-congruence |
| 1074 | (*β* = *−*9*.*56 *×* 10*−*3 ± 1*.*37 *×* 10*−*3, T(1*.*98 *×* 106) = *−*6*.*97, p = 3*.*15 *×* 10*−*12). |
| 1075 | H. The mode of perceptual processing (i.e., the difference between the smoothed probability |
| 1076 | of stimulus- vs. history-congruence) showed a quadratic relationship to RTs, with faster |
| 1077 | RTs for stronger biases toward both external sensory information and internal predictions |
| 1078 | provided by perceptual history (*β*2 = *−*19*.*86 ± 0*.*52, T(1*.*98 *×* 106) = *−*38*.*43, p = 5 *×* 10*−*323). |
| 1079 | The horizontal and vertical dotted lines indicate maximum RT and the associated mode, |
| 1080 | respectively. |
| 1081 | I. Confidence was enhanced for both stimulus-congruence (as opposed to stimulus- |

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incongruence, *β* = 0*.*48 ± 1*.*38 *×* 10*−*3, T(2*.*06 *×* 106) = 351*.*54, p < 2*.*2 *×* 10*−*308) and

history-congruence (*β* = 0*.*04 ± 1*.*18 *×* 10*−*3, T(2*.*06 *×* 106) = 36*.*85, p = 3*.*25 *×* 10*−*297).

J. In analogy to RTs, we found a quadratic relationship between the mode of perceptual processing and confidence, which increased when both externally- and internally-biased modes grew stronger (*β*2 = 39*.*3 ± 0*.*94, T(2*.*06 *×* 106) = 41*.*95, p < 2*.*2 *×* 10*−*308). The horizontal and vertical dotted lines indicate minimum confidence and the associated mode, respectively.

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## Figure 3

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**Figure 3. Internal and external modes in mouse perceptual decision-making.**

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| 1091 | A. In mice, 81.37% ± 0.3% of trials were stimulus-congruent (in red) and 54.03% ± 0.17% of |
| 1092 | trials were history-congruent (in blue; upper panel). History-congruent perceptual choices |
| 1093 | were not a consequence of the experimental design, but a source of error, as they were more |
| 1094 | frequent on stimulus-incongruent trials (lower panel). |
| 1095 | B. Relative to randomly permuted data, we found highly significant autocorrelations of |
| 1096 | stimulus-congruence and history-congruence (dots indicate intercepts *̸*= 0 in trial-wise linear |
| 1097 | mixed effects modeling at p < 0.05). Please note that the negative autocorrelation of |
| 1098 | stimulus-congruence at trial 2 was a consequence of the experimental design (Supplemental |
| 1099 | Figure 2D-F). As in humans, autocorrelation coefficients were best fit by an exponential |
| 1100 | function (adjusted *R*2 for stimulus-congruence: 0*.*44; history-congruence: 0*.*52) as compared |
| 1101 | to a linear function (adjusted *R*2 for stimulus-congruence: 3*.*16 *×* 10*−*3; history-congruence: |

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| 1102 | 0*.*26), decaying at a rate of *γ* = *−*6*.*2 *×* 10*−*4 ± 5*.*93 *×* 10*−*4 (T(3*.*55 *×* 104) = *−*1*.*05, p = 0*.*3) |
| 1103 | for stimulus-congruence and at a rate of *γ* = *−*6*.*7 *×* 10*−*3 ± 5*.*94 *×* 10*−*4 (T(3*.*69 *×* 104) = |
| 1104 | *−*11*.*27, p = 2*.*07 *×* 10*−*29) for history-congruence. |
| 1105 | C. For stimulus-congruence (upper panel), the lag of positive autocorrelation was longer in |
| 1106 | comparison to humans (4.59 ± 0.06 on average). For history-congruence (lower panel), the |
| 1107 | lag of positive autocorrelation was slightly shorter relative to humans (2.58 ± 0.01 on average, |
| 1108 | peaking at trial t+2 after the index trial). |
| 1109 | D. In mice, the dynamic probabilities of stimulus- and history-congruence (sliding windows |
| 1110 | of ±5 trials) fluctuated as **a scale-invariant process with a 1/f power law**. |
| 1111 | E. The distribution of phase shift between fluctuations in stimulus- and history-congruence |
| 1112 | peaked at half a cycle (*π* denoted by dotted line). |
| 1113 | F. The average squared coherence between fluctuations in stimulus- and history-congruence |
| 1114 | (black dotted line) amounted to 3.45 ± 0.01%. |
| 1115 | G. We observed shorter trial durations (TDs) for stimulus-congruence (as opposed to stimulus- |
| 1116 | incongruence, *β* = *−*1*.*12 ± 8*.*53 *×* 10*−*3, T(1*.*34 *×* 106) = *−*131*.*78, p < 2*.*2 *×* 10*−*308), but |
| 1117 | longer TDs for history-congruence (*β* = 0*.*06 ± 6*.*76 *×* 10*−*3, T(1*.*34 *×* 106) = 8*.*52, p = |
| 1118 | 1*.*58 *×* 10*−*17). |
| 1119 | H. TDs decreased monotonically for stronger biases toward external mode (*β*1 = *−*4*.*16 *×* 104 |
| 1120 | ± 1*.*29 *×* 103, T(1*.*35 *×* 106) = *−*32*.*31, p = 6*.*03 *×* 10*−*229). The horizontal and vertical dotted |
| 1121 | lines indicate maximum TD and the associated mode, respectively. |
| 1122 | I. For TDs that differed from the median TD by no more than 1.5 x MAD (median absolute |
| 1123 | distance49), mice exhibited a quadratic component in the relationship between the mode of |
| 1124 | sensory processing and TDs (*β*2 = *−*1*.*97 *×* 103 ± 843*.*74, T(1*.*19 *×* 106) = *−*2*.*34, p = 0*.*02). |
| 1125 | This explorative post-hoc analysis focuses on trials at which mice engage more swiftly with |
| 1126 | the experimental task. The horizontal and vertical dotted lines indicate maximum TD and |

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the associated mode, respectively.

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## Figure 4

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**Figure 4. Internal and external modes in simulated perceptual decision-making.**

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| 1131 | A. Simulated perceptual choices were stimulus-congruent in 71.36% ± 0.17% (in red) and |
| 1132 | history-congruent in 51.99% ± 0.11% of trials (in blue; T(4*.*32*×*103) = 17*.*42, p = 9*.*89*×*10*−*66; |
| 1133 | upper panel). Due to the competition between stimulus- and history-congruence, history- |
| 1134 | congruent perceptual choices were more frequent when perception was stimulus-incongruent |
| 1135 | (i.e., on *error* trials; T(4*.*32 *×* 103) = 11.19, p = 1*.*17 *×* 10*−*28; lower panel) and thus impaired |
| 1136 | performance in the randomized psychophysical design simulated here. |
| 1137 | B. At the simulated group level, we found significant autocorrelations in both stimulus- |
| 1138 | congruence (13 consecutive trials) and history-congruence (30 consecutive trials). |
| 1139 | C. On the level of individual simulated participants, autocorrelation coefficients exceeded the |
| 1140 | autocorrelation coefficients of randomly permuted data within a lag of 2*.*46 ± 1*.*17 *×* 10*−*3 |

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| 1141 | trials for stimulus-congruence and 4*.*24 ± 1*.*85 *×* 10*−*3 trials for history-congruence. |
| 1142 | D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ±5 |
| 1143 | trials) fluctuated as **a scale-invariant process with a 1/f power law**, i.e., at power |
| 1144 | densities that were inversely proportional to the frequency (power ~ 1/*fβ*; stimulus-congruence: |
| 1145 | *β* = *−*0*.*81 ± 1*.*18 *×* 10*−*3, T(1*.*92 *×* 105) = *−*687*.*58, p < 2*.*2 *×* 10*−*308; history-congruence: *β* |
| 1146 | = *−*0*.*83 ± 1*.*27 *×* 10*−*3, T(1*.*92 *×* 105) = *−*652*.*11, p < 2*.*2 *×* 10*−*308). |
| 1147 | E. The distribution of phase shift between fluctuations in simulated stimulus- and history- |
| 1148 | congruence peaked at half a cycle (*π* denoted by dotted line). The dynamic probabilities of |
| 1149 | simulated stimulus- and history-congruence were therefore were strongly anti-correlated (*β* = |
| 1150 | *−*0*.*03 ± 8*.*22 *×* 10*−*4, T(2*.*12 *×* 106) = *−*40*.*52, p < 2*.*2 *×* 10*−*308). |
| 1151 | F. The average squared coherence between fluctuations in simulated stimulus- and history- |
| 1152 | congruence (black dotted line) amounted to 6*.*49 ± 2*.*07 *×* 10*−*3%. |
| 1153 | G. Simulated confidence was enhanced for stimulus-congruence (*β* = 0*.*03 ± 1*.*71 *×* 10*−*4, |
| 1154 | T(2*.*03 *×* 106) = 178*.*39, p < 2*.*2 *×* 10*−*308) and history-congruence (*β* = 0*.*01 ± 1*.*5 *×* 10*−*4, |
| 1155 | T(2*.*03 *×* 106) = 74*.*18, p < 2*.*2 *×* 10*−*308). |
| 1156 | H. In analogy to humans, the simulated data showed a quadratic relationship between the |
| 1157 | mode of perceptual processing and posterior certainty, which increased for stronger external |
| 1158 | and internal biases (*β*2 = 31*.*03 ± 0*.*15, T(2*.*04 *×* 106) = 205*.*95, p < 2*.*2 *×* 10*−*308). The |
| 1159 | horizontal and vertical dotted lines indicate minimum posterior certainty and the associated |
| 1160 | mode, respectively. |

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**Supplemental Information**

Supplement\_clean.pdf: Supplemental Items and Figures

Supplement\_track\_changes.pdf: Supplemental Items and Figures with tracked changes

The above files contain the following supplemental items and figures:

**Supplemental Text Items**

1. Internal mode processing is driven by choice history as opposed to stimulus history
2. Internal mode is characterized by lower thresholds as well as by history-dependent changes

in biases and lapses

1. Internal mode processing can not be reduced to insufficient task familiarity

**Supplemental Figures**

1. Supplemental Figure S1. Stimulus- and history-congruence.
2. Supplemental Figure S2. Controlling for task difficulty and external stimulation
3. Supplemental Figure S3. Reproducing group-level autocorrelations using logistic regression
4. Supplemental Figure S4. History-congruence in logistic regression.
5. Supplemental Figure S5. Correcting for general response biases
6. Supplemental Figure S6. Full and history-conditioned psychometric functions across modes

in humans

1. Supplemental Figure S7. Full and history-conditioned psychometric functions across modes

in mice

1. Supplemental Figure S8. History-/stimulus-congruence and TDs during training of the basic task
2. Supplemental Figure S9. Comparison of the bimodal inference model against reduced control models
3. Supplemental Figure S10. Reduced Control Model M2: Only oscillation of the likelihood
4. Supplemental Figure S11. Reduced Control Model M3: Only oscillation of the prior
5. Supplemental Figure S12. Reduced Control Model M4: Normative evidence accumulation
6. Supplemental Figure S13. Reduced Control Model M5: No accumulation of information across trials.
7. Supplemental Figure S14. Autocorrelation of history-congruence of alternating and repeating biases

**Supplemental Tables**

1. Supplemental Table T1. Studies extracted from the Confidence Database
2. Supplemental Table T2. Explanation of model parameters