# 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

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

12 are 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 not behave more

43 randomly, but showed stronger serial dependencies in their perceptual choices22–33. These

44 serial dependencies may be understood as driven by internal predictions that reflect the auto-

45 correlation of natural environments34 and bias perception toward preceding experiences30,31,35.

46 Computational modeling indicated that ongoing changes in perceptual performance may

47 be driven by systematic fluctuations between externally- and internally-oriented *modes* of

48 sensory analysis. We suggest that such *bimodal inference* may help to build stable internal

49 representations of the sensory environment despite an ongoing stream of sensory information.

50 **5 Results**

## 51 5.1 Human perception fluctuates between epochs of enhanced and

52 **reduced sensitivity to external information**

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

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

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

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

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

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

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

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

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

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

63 the selected studies (Supplemental Figure S1A). In line with previous work8, we found that

64 the probability of stimulus-congruence was not independent across successive trials: At the

65 group level, stimulus-congruent perceptual choices were significantly autocorrelated for up

66 to 15 trials (Figure 2B), controlling for task difficulty and the sequence of presented stimuli

67 (Supplemental Figure 2A-B).

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

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

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

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

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

73 autocorrelation of stimulus-congruence was corroborated by logistic regression models that

74 successfully predicted the stimulus-congruence of perception at the index trial *t* = 0 from the

75 stimulus-congruence at the preceding trials within a lag of 16 trials (Supplemental Figure

76 S3).

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

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

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

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

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

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

83 a power density that was inversely proportional to the frequency in the slow spectrum11

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

85 2D). This feature, which is also known as a *1/f power law*36,37, represents a characteristic

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

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

## 88 5.2 Humans fluctuate between external and internal modes of

89 **sensory processing**

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

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

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

93 are constructed from previous experiences19,31.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

109 (56.03% ± 0.2%) as opposed to stimulus-congruent (51.77% ± 0.11%, *β* = *−*4*.*26 ± 0*.*21,

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

111 autocorrelated real-world environments19,34,35,42, perceptual history thus represented a source

112 of bias in the randomized experimental designs studied here24,28,30,31,43. These serial biases

113 were effects of choice history, i.e., driven by the experiences reported at the preceding trial,

114 and could not be attributed to stimulus history, i.e., to effects of the stimuli presented at the

115 preceding trial (Supplemental Section 1.1).

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

117 is characterized by stronger or weaker biases toward preceding experiences. In close analogy

118 to stimulus-congruence, we found history-congruence to be significantly autocorrelated for up

119 to 21 trials (Figure 2B), while controlling for task difficulty and the sequence of presented

120 stimuli (Supplemental Figure 2A-B). In individual participants, the autocorrelation of history-

121 congruence was elevated above randomly permuted data for a lag of 4*.*87 ± 3*.*36 *×* 10*−*3

122 trials (Figure 2C), confirming that the autocorrelation of history-congruence was not only

123 a group-level phenomenon. The autocorrelation of history-congruence was corroborated by

124 logistic regression models that successfully predicted the history-congruence of perception at

125 an index trial *t* = 0 from the history-congruence at the preceding trials within a lag of 17

126 trials (Supplemental Figure S3).

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

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

129 sensitivity to external information9,10,13,39,40). The dynamic probability of history-congruent

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

131 over time, ranging between a minimum of 12.77% ± 0.14% and a maximum 92.23% ± 0.14%.

132 In analogy to stimulus-congruence, we found that history-congruence fluctuated as at power

133 densities that were inversely proportional to the frequency in the slow spectrum11 (power ~

134 1/*fβ*, *β* = *−*1*.*34 ± 3*.*16 *×* 10*−*3, T(1*.*84 *×* 105) = *−*423*.*91, p < 2*.*2 *×* 10*−*308; Figure 2D).

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

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

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

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

139 fluctuations in general response biases; Supplemental Section 1.2). Thus, while sharing the

140 1/f power law characteristic, fluctuations in stimulus- and history-congruence were shifted

141 against each other by approximately half a cycle and showed a squared coherence of 6*.*49 ±

142 2*.*07 *×* 10*−*3% (Figure 2E and F; we report the average phase and coherence for frequencies

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

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

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

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

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

148 profiles.

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

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

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

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

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

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

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

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

157 information4,5,18.

## 158 5.3 Internal and external modes of processing facilitate response

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

160 **making**

161 The above results point to systematic fluctuations in the *decision variable*44 that determines

162 perceptual choices, causing enhanced sensitivity to external stimulus information during

163 external mode and increased biases toward preceding choices during internal mode. As such,

164 fluctuations in mode should influence downstream aspects of behavior and cognition that

165 operate on the perceptual decision variable44. To test this hypothesis with respect to motor

166 behavior and metacognition, we asked how bimodal inference relates to response times (RTs)

167 and confidence reports.

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

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

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

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

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

173 Figure 2G).

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

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

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

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

178 *−*38*.*43, p = 5 *×* 10*−*323), participants became faster at indicating their perceptual decision

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

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

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

182 3*.*25 *×* 10*−*297; Figure 2I). Yet whilst controlling for the effect of stimulus-congruence, we found

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

184 351*.*54, p < 2*.*2 *×* 10*−*308; Figure 2I).

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

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

187 = 92*.*89, p < 2*.*2 *×* 10*−*308). Importantly, however, participants were more confident in their

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

189 0*.*94, T(2*.*06 *×* 106) = 41*.*95, p < 2*.*2 *×* 10*−*308). In analogy to RTs, subjective confidence thus

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

210 In what follows, we probe alternative explanations for between-mode fluctuations, test for

211 the existence of modes in mice, and propose a predictive processing model that explains

212 fluctuations in mode ongoing shifts in the precision afforded to external sensory information

213 relative to internal predictions driven by perceptual history.

## 214 5.4 Fluctuations between internal and external mode cannot be

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

216 The core assumption of bimodal inference - that ongoing changes in the sensitivity to external

217 information are driven by internal predictions induced via perceptual history - needs to

218 be contrasted against two alternative hypotheses: When making errors, observers may not

219 engage with the task and respond stereotypically, i.e., exhibit stronger general biases toward

220 one of the two potential outcomes, or simply choose randomly.

221 Logistic regression confirmed that perceptual history made a significant contribution to

222 perception (*β* = 0*.*11 ± 5*.*79 *×* 10*−*3, z = 18*.*53, p = 1*.*1 *×* 10*−*76) over and above the ongoing

223 stream of external sensory information (*β* = 2*.*2 ± 5*.*87 *×* 10*−*3, z = 375*.*11, p < 2*.*2 *×* 10*−*308)

224 and general response biases toward (*β* = 15*.*19 ± 0*.*08, z = 184*.*98, p < 2*.*2 *×* 10*−*308).

225 When eliminating perceptual history as a predictor of individual choices at individual trials,

226 Akaike Information Criterion (AIC48) increased by *δAIC* = 1*.*64 *×* 103 (see Supplemental

227 Figure S4A-B for parameter- and model-level inference at the level of individual observers).

228 Likewise, when eliminating slow fluctuations in history-congruence as a predictor of slow

229 fluctuations in stimulus-congruence across trials, we observed an increase in AIC by *δAIC*

230 = 7*.*06 *×* 103. These results provided model-level evidence against the null hypotheses that

231 fluctuations in stimulus-congruence are driven exclusively by choice randomness or general

232 response bias (see Supplemental Section 1.2 and Supplemental Figure S5 for an in-depth

233 assessment of general response bias).

234 To confirm that changes in the sensitivity to external information are indicative of internal

235 mode processing, we estimated full and history-dependent psychometric curves during internal,

236 external, and across modes21. If, as we hypothesized, internal mode processing reflects an

237 enhanced impact of perceptual history, one would expect a history-dependent increase in

238 biases and lapses as well as a history-independent increase in threshold. Conversely, if internal

239 mode processing were driven by random choices, one would expect a history-independent

240 increase in lapses and threshold, and no change in bias. In line with our prediction, we found

241 that internal mode processing was associated with a history-dependent increase in bias and

242 lapse as well as a history-independent increase in threshold (Supplemental Section 1.3.1 and

243 Supplemental Figure S6). This confirmed that internal mode processing is indeed driven by

244 an enhanced impact of perceptual history.

245 In line with this, the quadratic relationship between mode and confidence (Figure 2J)

246 suggested that biases toward internal information do not reflect a post-perceptual strategy

247 of repeating preceding choices when the subjective confidence in the perceptual decision is

248 low. Moreover, while responses became faster with longer exposure to the experiments of the

249 Confidence database, the frequency of history-congruent choices increased over time, speaking

250 against the proposition that participants stereotypically repeat preceding choices when not

251 yet familiar with the experimental task (Supplemental Section 1.4.1).

252 Taken together, our results thus argue against recurring intervals of low task engagement,

253 which may be signaled by stereotypical or random responses, as an alternative explanation

254 for the phenomenon that we identify as bimodal inference.

## 255 5.5 Mice fluctuate between external and internal modes of sensory

256 **processing**

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

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

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

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

261 choices should not be a uniquely human phenomenon.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

278 confirming that perceptual history was a source of bias24,28,30,31,43 as opposed to a feature of

279 the experimental paradigm.

280 At the group level, we found significant autocorrelations in both stimulus-congruence (42

281 consecutive trials) and history-congruence (8 consecutive trials; Figure 3B), while controlling

282 for the respective autocorrelation of task difficulty and external stimulation (Supplemental

283 Figure 2C-D). In contrast to humans, mice showed a negative autocorrelation coefficient

284 of stimulus-congruence at trial 2, which was due to a feature of the experimental design:

285 Errors at a contrast above 50% were followed by a high-contrast stimulus at the same

286 location. Thus, stimulus-incongruent choices on easy trials were more likely to be followed by

287 stimulus-congruent perceptual choices that were facilitated by high-contrast visual stimuli21.

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

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

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

291 regression models that successfully predicted the stimulus-/history-congruence of perception

292 at the index trial *t* = 0 from the stimulus-/history-congruence at the 33 preceding trials for

293 stimulus-congruence and 8 preceding trials for history-congruence (Supplemental Figure S3).

294 In analogy to humans, mice showed anti-phase 1/f fluctuations in the sensitivity to internal

295 and external information (Figure 3D-F).

296 The above results confirm that fluctuations between internally- and externally-biased modes

297 generalize to perceptual decision-making in mice. Following our hypothesis that bimodal

298 inference operates at the level of perception, we predicted that between-mode fluctuations

299 modulate a decision variable44 that determines not only perceptual choices, but also down-

300 stream aspects of mouse behavior44. We therefore asked how external and internal modes

301 relate to the trial duration (TD, a coarse measure of RT in mice that spans the interval

302 from stimulus onset to feedback21). Stimulus-congruent (as opposed to stimulus-incongruent)

303 choices were associated with shorter TDs (*δ* = *−*262*.*48 ± 17*.*1, T(164) = -15.35, p =

304 1*.*55 *×* 10*−*33), while history-congruent choices were characterized by longer TDs (*δ* = 30*.*47

305 ± 5*.*57, T(164) = 5.47, p = 1*.*66 *×* 10*−*7; Figure 3G).

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

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

308 1*.*29 *×* 103, T(1*.*35 *×* 106) = *−*32*.*31, p = 6*.*03 *×* 10*−*229, Figure 3H). However, an explorative

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

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

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

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

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

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

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

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

317 for external sensory information (*β* = 2*.*96 ± 4*.*58 *×* 10*−*3, z = 646*.*1, p < 2*.*2 *×* 10*−*308) and

318 general response biases toward one of the two outcomes (*β* = *−*1*.*78 ± 0*.*02, z = *−*80*.*64, p

319 < 2*.*2 *×* 10*−*308). When eliminating perceptual history as a predictor of individual choices,

320 AIC increased by *δAIC* = 1*.*48 *×* 104, arguing against the notion that choice randomness

321 and general response bias are the only determinants of perceptual performance in mice (see

322 Supplemental Figure S4C-D for parameter- and model-level inference in individual subjects).

323 In mice, fluctuations in the strength of history-congruent biases had a significant effect on

324 stimulus-congruence (*β*1 = *−*0*.*12 ± 7*.*17 *×* 10*−*4, T(1*.*34 *×* 106) = *−*168*.*39, p < 2*.*2 *×* 10*−*308)

325 beyond the effect of ongoing changes in general response biases (*β*2 = *−*0*.*03 ± 6*.*94 *×* 10*−*4,

326 T(1*.*34 *×* 106) = *−*48*.*14, p < 2*.*2 *×* 10*−*308). Eliminating the dynamic fluctuations in history-

327 congruence as a predictor of fluctuations in stimulus-congruence resulted in an increase in

328 AIC by *δAIC* = 2*.*8 *×* 104 (see Supplemental Section 1.2 and Supplemental Figure S5 for an

329 in-depth assessment of general response bias).

330 When fitting full and history-conditioned psychometric curves to the IBL data21, we observed

331 that internal mode processing was associated with a history-dependent increase in bias and

332 lapse as well as a history-independent increase in threshold (Supplemental Section 1.3.2 and

333 Supplemental Figure S7). Over time, the frequency of history-congruent choices increased

334 alongside stimulus-congruence and speed of response as mice were exposed to the experiment,

335 arguing against the proposition that biases toward perceptual history reflected an unspecific

336 response strategy in mice who were not sufficiently trained on the IBL task (Supplemental

337 Section 9.4.2 and Supplemental Figure S8).

338 In sum, these analyses confirmed that the observed fluctuations in sensitivity to external

339 sensory information are driven by dynamic changes in impact of perceptual history and

340 cannot be reduced to general response bias and random choice behavior.

## 341 5.6 Fluctuations in mode result from coordinated changes in the

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

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

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

345 enhanced sensitivity toward either external sensory information or internal predictions

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

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

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

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

350 time50.

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

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

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

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

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

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

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

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

359 decision variable from implicit internal representations of the environment19.

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

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

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

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

364 respective precision terms *ωLLR* and *ωψ*:

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

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

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

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

368 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)

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

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

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

1

= 1 + *exp*(*−α ∗ s* ) (3)

*ut*

*t*

*LLR* = *log*( *ut*

*t* 1

*− ut*

) (4)

372 To allow for bimodal inference, i.e., alternating periods of internally- and externally-biased

373 modes of perceptual processing that occur irrespective of the sequence of preceding experiences,

374 we assumed that likelihood and prior vary in their influence on the perceptual decision

375 according to fluctuations governed by *ωLLR* and *ωψ*. These anti-phase sine functions (defined

376 by amplitudes *aLLR/ψ*, frequency *f* and phase *p*) determine the precision afforded to the

377 likelihood and prior53. The implicit anti-phase fluctuations are mandated by Bayes-optimal

378 formulations in which inference depends only on the relative values of prior and likelihood

379 precision (i.e., the Kalman gain54). As such, *ωLLR* and *ωψ* implement a hyperprior55 in which

380 the likelihood and prior precisions are shifted against each other at a dominant timescale

381 defined by *f* :

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

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

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

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

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*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 Methods for details and Supplemental Table T2 for a summary of the parameters of the bimodal inference model). We validated our model in three steps:

First, to show that bimodal inference does not emerge spontaneously in normative Bayesian models of evidence accumulation, but requires the ad-hoc addition of anti-phase oscillations in prior and likelihood precision, we compared the bimodal inference model to four control models (M2-5, Figure 1G). In these models, we successively removed the anti-phase oscillations (M2-M4) and the integration of information across trials (M5) from the bimodal inference model and performed a model comparison based on AIC.

Model M2 (*AIC*2 = 9*.*76 *×* 104 in humans and 4*.*91 *×* 104 in mice) and Model M3 (*AIC*3 = 1*.*19 *×* 105 in humans and 5*.*95 *×* 104 in mice) incorporated only oscillations of either likelihood or prior precision. Model M4 (*AIC*4 = 1*.*69 *×* 105 in humans and 9*.*12 *×* 104 in mice) lacked any oscillations of likelihood and prior precision and corresponded to the normative model proposed by Glaze et al.51. In model M5 (*AIC*4 = 2*.*01 *×* 105 in humans and 1*.*13 *×* 105

in mice), we furthermore removed the integration of information across trials, such that perception depended only in incoming sensory information (Figure 1G).

The bimodal inference model achieved the lowest AIC across the full model space (*AIC*1

= 8*.*16 *×* 104 in humans and 4*.*24 *×* 104 in mice) and was clearly superior to the normative Bayesian model of evidence accumulation (*δAIC* = *−*8*.*79 *×* 104 in humans and *−*4*.*87 *×* 104 in mice; Supplemental Figure S9).

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

407 model predicted within-training and out-of-training variables. The bimodal inference model

408 characterizes each subject by a sensitivity parameter *α* (humans: *α* = 0*.*5 ± 1*.*12 *×* 10*−*4; mice:

409 *α* = 1*.*06 ± 2*.*88 *×* 10*−*3) that captures how strongly perception is driven by the available

410 sensory information, and a hazard rate parameter *H* (humans: *H* = 0*.*45 ± 4*.*8 *×* 10*−*5; mice:

411 *H* = 0*.*46 ± 2*.*97 *×* 10*−*4) that controls how heavily perception is biased by perceptual history.

412 The parameter *f* captures the dominant time scale at which likelihood (amplitude humans:

413 *aLLR* = 0*.*5 ± 2*.*02 *×* 10*−*4; mice: *aLLR* = 0*.*39 ± 1*.*08 *×* 10*−*3) and prior precision (amplitude

414 humans: *aψ* = 1*.*44 ± 5*.*27 *×* 10*−*4; mice: *aψ* = 1*.*71 ± 7*.*15 *×* 10*−*3) fluctuated and was

415 estimated at 0*.*11 ± 1*.*68 *×* 10*−*5 1/*Ntrials* and 0*.*11 ± 1*.*63 *×* 10*−*4 1/*Ntrials* in mice.

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

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

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

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

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

421 ± 0*.*12, T(2*.*07 *×* 103) = 16*.*21, p = 9*.*37 *×* 10*−*56). Likewise, *H* was negatively correlated

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

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

424 p = 1*.*85 *×* 10*−*20).

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

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

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

428

hazard rate *H*ˆ

of the experimental environments (Confidence database20:

*H*ˆ*Humans* = 0*.*5

429

± 1*.*58 *×* 10*−*5); IBL database21:

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

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

431

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

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

432 *−*7*.*33, p = 5*.*76 *×* 10*−*10) and mice (*β* = *−*2*.*91 ± 0*.*34, T(112*.*57) = *−*8*.*51, p = 8*.*65 *×* 10*−*14).

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

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

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

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

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

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

439 = *−*9*.*41, p = 5*.*19 *×* 10*−*21) and TDs mice (*β* = *−*35*.*45 ± 0*.*86, T(1*.*28 *×* 106) = *−*41*.*13, p

440 < 2*.*2 *×* 10*−*308). Likewise, subjective confidence reports were positively correlated with the

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

442 = 9*.*18, p = 4*.*48 *×* 10*−*20).

443 The dynamic accumulation of information inherent to our model entails that biases toward

444 perceptual history are stronger when the posterior decision certainty at the preceding trial is

445 high30,31,51. Due to the link between posterior decision certainty and confidence, confident

446 perceptual choices should be more likely to induce history-congruent perception at the

447 subsequent trial30,31. In line with our prediction, logistic regression indicated that history-

448 congruence was predicted by the posterior decision certainty *|Lt−*1*|* extracted from the model

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

450 1*.*83 *×* 10*−*3, z = *−*2*.*03, p = 0*.*04) and the subjective confidence reported by the participants

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

452 As a third validation of the bimodal inference model, we used the posterior model parameters

453 to simulate synthetic perceptual choices and repeated the behavioral analyses conducted

454 for the empirical data. Simulations from the bimodal inference model closely replicated our

455 empirical results: Simulated perceptual decisions resulted from a competition of perceptual

456 history with incoming sensory signals (Figure 4A). Stimulus- and history-congruence were

457 significantly autocorrelated (Figure 4B-C), fluctuating in anti-phase as a scale-invariant

458 process with a 1/f power law (Figure 4D-F). Simulated posterior certainty28,30,44 (i.e., the

459 absolute of the log posterior ratio *|Lt|*) showed a quadratic relationship to the mode of sensory

460 processing (Figure 4H), mirroring the relation of RTs and confidence reports to external and

461 internal biases in perception (Figure 2G-H and Figure 3G-H). Crucially, the overlap between

462 empirical and simulated data broke down when we removed the anti-phase oscillations or the

463 accumulation of evidence over time from the bimodal inference model (Supplemental Figures

464 S10-13).

465 In sum, computational modeling suggested that between-mode fluctuations are best explained

466 by two interlinked processes (Figure 1E and F): (i), the dynamic accumulation of information

467 across successive trials mandated by normative Bayesian models of evidence accumulation

468 and, (ii), ongoing anti-phase oscillations in the impact of external and internal information.

469 **6 Discussion**

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

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

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

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

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

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

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

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

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

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

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

481 oriented modes of sensory analysis.

## 482 6.1 Bimodal inference represents a pervasive aspect of perceptual

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

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

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

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

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

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

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

490 in humans (Figure 2I).

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

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

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

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

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

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

497 perceptual performance6–11.

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

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

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

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

502 sequential Bayes25,42,51 such as Kalman35 or Hierarchical Gaussian filtering54. At the level of

503 neural mechanisms, the integration of internal with external information may be realized by

504 combining feedback from higher levels in the cortical hierarchy with incoming sensory signals

505 that are fed forward from lower levels56.

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

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

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

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

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

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

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

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

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

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

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

517 and reality monitoring59.

518 We hypothesized that observers have certain hyperpriors that are apt for accommodating

519 fluctuations in the predictability of their environment, i.e., people believe that their world is

520 inherently volatile. To be Bayes optimal, it is therefore necessary to periodically re-evaluate

521 posterior beliefs about the parameters that define an internal generative model of the external

522 sensory environment. One way to do this is to periodically suspend the precision of prior

523 beliefs and increase the precision afforded to sensory evidence, thus updating Bayesian beliefs

524 about model parameters.

525 The empirical evidence above suggests that the timescale of this periodic scheduling of

526 evidence accumulation may be scale-invariant. This means that there may exist a timescale

527 of periodic fluctuations in precision over every window or length of perceptual decision-

528 making. Bimodal inference predicts perceptual decisions under a generative model (based

529 upon a hazard function to model serial dependencies between subsequent trials) with periodic

530 fluctuations in the precision of sensory evidence relative to prior beliefs at a particular

531 timescale. Remarkably, a systematic model comparison based on AIC indicated that a model

532 with fluctuating precisions has much greater evidence, relative to a model in the absence of

533 fluctuating precisions. This ad-hoc addition of oscillations to a normative Bayesian model of

534 evidence accumulation51 allowed us to quantify the dominant timescale of periodic fluctuations

535 mode at approximately 0.11 1/*Ntrials* in humans and mice that is appropriate for these kinds

536 of paradigms.

## 537 6.2 Bimodal inference versus normative Bayesian evidence accu-

538 **mulation**

539 Could bimodal inference emerge spontaneously in normative models of perceptual decision-

540 making? In predictive processing, the relative precision of prior and likelihood determines

541 their integration into the posterior that determines the content of perception. At the level

542 of individual trials, the perceptual impact of internal predictions generated from perceptual

543 history (prior precision) and external sensory information (likelihood precision) are thus

544 necessarily anti-correlated. The same holds for mechanistic models of drift diffusion, which

545 understand choice history biases as driven by changes in the starting point51 or the drift rate

546 of evidence accumulation32. Under the former formulation, perceptual history is bound to

547 have a stronger influence on perception when less weight is given to incoming sensory evidence,

548 assuming that the last choice is represented as a starting point bias. The effects of choice

549 history in normative Bayesian and mechanistic drift diffusion models can be mapped onto

550 one another via the Bayesian formulation of drift diffusion60, where the inverse of likelihood

551 precision determines the amount of noise in the accumulation of new evidence, and prior

552 precision determines the absolute shift in its starting point60.

553 While it is thus clear that the impact of perceptual history and sensory evidence are anti-

554 correlated *at each individual trial*, we here introduce anti-phase oscillations as an ad-hoc

555 modification to model slow fluctuations in prior and likelihood precision that evolve *over*

556 *many consecutive trials* and are not mandated by normative Bayesian or mechanistic drift

557 diffusion models. The bimodal inference model provides a reasonable explanation of the

558 linked autocorrelations in stimulus- and history-congruence, as evidenced by formal model

559 comparison, successful prediction of RTs and confidence as out-of-training variables, and a

560 qualitative reproduction of our empirical data from posterior model parameter as evidence

561 against over- or under-fitting.

562 Of note, similar non-stationarities have been observed in descriptive models that assume

563 continuous61 or discrete12 changes in the latent states that modulate perceptual decision-

564 making at slow timescales. A recent computational study62 has used a Hidden Markov model

565 to investigate perceptual decision-making in the IBL database21. In analogy to our findings,

566 the authors observed that mice switch between temporally extended *strategies* that last for

567 more than 100 trials: During *engaged* states, perception was highly sensitive to external

568 sensory information. During *disengaged* states, in turn, choice behavior was prone to errors

569 due to enhanced biases toward one of the two perceptual outcomes62. Despite the conceptual

570 differences to our approach (discrete states in a Hidden Markov model that correspond to

571 switches between distinct decision-making strategies62 vs. gradual changes in mode that

572 emerge from sequential Bayesian inference and ongoing oscillations in the impact of external

573 relative to internal information), it is tempting to speculate that engaged/disengaged states

574 and between-mode fluctuations might tap into the same underlying phenomenon.

## 575 6.3 Task engagement and residual motor activation as alternative

576 **explanations for bimodal inference**

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

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

579 of the sensory environment. Between-mode fluctuations may thus elude circular inferences

580 that occur when both the causes and the encoding of sensory stimuli are volatile19,57. By

581 the same token, we suggest that fluctuations in mode occur at the level of perceptual

582 processing26,30,46,47, and are not a passive phenomenon that is primarily driven by factors

583 situated up- or downstream of sensory analysis.

584 How does attention relate to phenomenon of between-mode fluctuations? According to

585 predictive processing, attention corresponds to the precision afforded to the probability

586 distributions that underlie perceptual inference53. From this perspective, fluctuations between

587 external and internal mode can be understood as ongoing shifts in the attention afforded to

588 either external sensory information (regulated via likelihood precision) or internal predictions

589 (regulated via prior precision). When the precision of either likelihood or prior increases,

590 posterior precision increases, which leads to faster RTs and higher confidence. Therefore, when

591 defined from the perspective of predictive processing as the precision afforded to likelihood

592 and prior53, fluctuations in attention may provide a plausible explanation for the quadratic

593 relationship of mode to RTs and confidence (Figure 2H and J; Figure 3I, Figure 4I).

594 Outside of the predictive processing field, attention is often understood in the context of

595 task engagement63, which varies according to the availability of cognitive resources that are

596 modulated by factors such as tonic arousal, familiarity with the task, or fatigue63. Our results

597 suggest that internal mode processing cannot be completely reduced to intervals of low task

598 engagement: In addition to shorter RTs and elevated confidence, choices during internal mode

599 were not random or globally biased, but driven by perceptual history (Supplemental Section).

600 Moreover, our computational model identified the dominant timescale of between-mode

601 fluctuations at 0.11 1/*Ntrials*, which may be compatible with fluctuations in arousal64, but is

602 faster than to be expected for the development of task familiarity or fatigue.

603 However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,

604 speed of response and confidence, it is important to consider that global modulators such

605 as tonic arousal are known to have non-linear effects on task performance65: In perceptual

606 tasks, performance seems so be highest during mid-level arousal, whereas low- and high-level

607 arousal lead to reduced accuracy and slower responses65. This contrasts with the effects of

608 bimodal inference, where accuracy increases linearly as one moves from internal to external

609 mode, and responses become faster at both ends of the mode spectrum.

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

611 and mice across domains66–68, including biases toward perceptual history28 that we implicate

612 in internal mode processing. While the increase in response speed and history congruence

613 over time (Supplemental Section 1.4) may argue against insufficient training as an alternative

614 explanation for internal mode processing, it may also be indicative of waning arousal. The

615 multiple mechanistic mappings to RTs and confidence warrant more direct measures of arousal

616 (such as pupil size28,65,66,68–70, motor behavior69,70, or neural data71) to better delineate bimodal

617 inference from fluctuations in global modulators of task performance.

618 Residual activation of the motor system may provide another contribution to serial biases

619 in perceptual choices72. Such motor-driven priming may lead to errors in randomized

620 psychophysical designs, resembling the phenomenon that we identify as internally-biased

621 processing73. Moreover, residual activation of the motor system may lead to faster responses,

622 and thus constitutes an alternative explanation for the quadratic relationship of mode with

623 RTs72. The observation of elevated confidence for stronger biases toward internal mode speaks

624 against the proposition that residual activation of the motor system is the primary driver of

625 serial choice biases, since strong motor-driven priming should lead to frequent lapses that are

626 typically associated reduced confidence74. Likewise, perceptual history effects have repeatedly

627 been replicated in experiments with counter-balanced stimulus-response mappings30: Feigin2021.

628 No-response paradigms, in which perceptual decision are inferred from eye-movements alone,

629 could help to better differentiate perceptual from motor-related effects. Likewise, video-

630 tracking of response behavior and neural recording from motor- and premotor, which has

631 recently been released for the IBL database[IBL2023], may provide further insight into the

632 relation of motor behavior to the perceptual phenomenon of between-mode fluctuations.

## 633 6.4 Limitations and open questions

634 Our results suggest bimodal inference as a pervasive aspect of perceptual decision-making

635 in humans and mice. However, a number of limitations and open questions have to be

636 considered:

637 First, this work sought to understand whether fluctuations between internal and external

638 mode, which we initially observed in an experiment on bistable perception in humans19,

639 represent a general phenomenon that occurs across a diverse set of perceptual decision-making

640 tasks. Our analysis of the Confidence database20 therefore collapsed across all available

641 experiments on binary perceptual decision-making. Individual experiments differed with

642 respect to the stimuli, the manipulation of difficulty, the timing of trials, and the way

643 responses were collected, but were highly comparable with respect to the central variables of

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

645 The variability across experiments, which we considered as random effects in all statistical

646 analyses, enabled us to assess whether bimodal inference represents a general phenomenon in

647 perceptual decision-making, but limited the precision at which we were able to investigate

648 the relation of mode to behavioral variables such as timing, task difficulty, RT or confidence.

649 This issue is partially resolved by our analyses of the IBL database, which replicated our

650 findings in an experiment that was highly standardized with respect to timing, task difficulty,

651 and behavioral read-out21. It will be an important task for future research to validate our

652 results on bimodal inference in a standardized dataset of comparable volume in humans,

653 which is, to our knowledge, not yet available.

654 Second, our results point to an attraction of perception toward preceding choices. Previous

655 work has shown that perceptual decision-making is concurrently affected by both attractive

656 and repulsive serial biases that operate on distinct time-scales and serve complementary

657 functions for sensory processing27,75,76: Short-term attraction may serve the decoding of noisy

658 sensory inputs and increase the stability of perception, whereas long-term repulsion may

659 enable efficient encoding and sensitivity to change27. In the data analyzed here, history biases

660 tended to be repetitive (Figure 2A, Figure 3A, Supplemental Figure S6 and S7), and only

661 2 of the 66 experiments of the Confidence database20 showed significant alternating biases

662 (Supplemental Figure S1). However, as we show in Supplemental Figure S14, fluctuations in

663 both alternating and repeating history biases generate overlapping autocorrelation curves.

664 Our analysis of between-mode fluctuations is therefore not tied exclusively to repeating biases,

665 but accommodates alternating biases as well, such that both may lead to internally-biased

666 processing and reduced sensitivity to external sensory information. Future work could apply

667 our approach to paradigms that boost alternating as opposed to repeating biases, as this

668 would help to better understand how repetition and alternation are linked in terms of their

669 computational function and neural implementation27.

670 A third open question concerns the computational underpinnings of bimodal inference. The

671 addition of slow anti-phase oscillations to the integration of prior and likelihood represents

672 an ad-hoc modification of a normative Bayesian model of evidence accumulation51. While the

673 bimodal inference model is supported by formal model comparison, the successful prediction of

674 out-of-training variables and the qualitative reproduction of our empirical data in simulations

675 from posterior model parameters, it is an important task for future research to test (i),

676 whether between-mode fluctuations can emerge spontaneously in hierarchical models of

677 Bayesian inference, (ii), whether modes are continuous19 or discrete62, and (iii), whether

678 bimodal inference can be causally manipulated by experimental variables. We speculate that

679 between-mode fluctuations may separate the perceptual contribution of internal predictions

680 and external sensory data in time, creating unambiguous learning signals that benefit inference

681 about the precision of prior and likelihood, respectively. This proposition should be tested

682 empirically by relating the phenomenon of bimodal inference to performance in, e.g., reversal

683 learning, probabilistic reasoning, or metacognition.

684 A final important avenue for further research on bimodal inference is to elucidate its neurobi-

685 ological underpinnings. Since between-mode fluctuations were found in humans and mice,

686 future studies can apply non-invasive and invasive neuro-imaging and electrophysiology to

687 better understand the neural mechanisms that generate ongoing changes in mode in terms of

688 their neuro-anatomy, -chemistry and -circuitry.

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

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

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

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

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

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

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

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

697 failures and a departure from consensual reality79.

698 **7 Methods**

## 699 7.1 Resource availability

### 700 7.1.1 Lead contact

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

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

### 703 7.1.2 Materials availability

704 This study did not generate new unique reagents.

### 705 7.1.3 Data and code availability

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

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

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

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

## 710 7.2 Experimental model and subject details

### 711 7.2.1 Confidence database

712 We downloaded the human data from the Confidence database20 on 10/21/2020, limiting

713 our analyses to the category *perception*. Within this category, we selected studies in which

714 participants made binary perceptual decisions between two alternatives. We excluded two

715 experiments in which the average perceptual accuracy fell below 50%. After excluding

716 these experiments, our sample consisted of 21*.*05 million trials obtained from 4317 human

717 participants and 66 individual experiments (Supplemental Table 1). Out of the 66 included

718 experiments, 62 investigated visual, 1 auditory, 2 proprioceptive, and 1 multimodal perception.

719 59 experiments were based on discrimination and 6 on detection, with one investigating both.

### 720 7.2.2 IBL database

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

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

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

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

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

## 726 7.3 Method details

### 727 7.3.1 Variables of interest

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

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

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

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

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

733 windows of ±5 trials.

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

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

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

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

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

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

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

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

742 information on RTs, 46 cued the response by the onset of a response screen or an additional

743 response cue, whereas 14 allowed participants to response at any time after stimulus onset.

744 If RTs were available for both the perceptual decision and the confidence report, we only

745 extracted the RT associated with the perceptual decision. To enable comparability between

746 studies, we normalized RTs and confidence reports within individual studies using the *scale*

747 R function. If not available for a particular study, RTs were treated as missing variables.

748 From the IBL database21, we extracted trial durations (TDs) as defined by interval between

749 stimulus onset and feedback, which represents a coarse measure of RT21.

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

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

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

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

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

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

### 756 7.3.2 Control variables

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

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

759 In the Confidence Database20, 21 of the 66 included experiments used fixed difficulty levels,

760 whereas 45 manipulated difficulty levels within participants. Difficulty was manipulated via

761 noise masks, contrast, luminance, presentation time, or stimulus probability for gabors, dot

762 coherence for random dot kinematograms, difference in elements and set size for comparisons

763 of numerosity, difference in clicks for auditory discrimination, temporal distance for meta-

764 contrast masking, and amount of self-motion for proprioception. We treated task difficulty as

765 a missing variable for the experiments that fixed it at the participant-level, as this precluded

766 the computation of autocorrelation curves. In analogy to RTs and confidence, difficulty levels

767 were normalized within individual studies. For the IBL Database21, task difficulty was defined

768 by the contrast of the presented grating.

### 769 7.3.3 Autocorrelations

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

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

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

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

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

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

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

777 observed for randomly permuted data and averaged across participants.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

794 the respective permuted autocorrelation coefficients.

### 795 7.3.4 Spectral analysis

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

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

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

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

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

801 a width of 50.

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

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

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

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

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

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

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

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

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

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

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

## 813 7.4 Quantification and statistical procedures

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

815 the mean.

### 816 7.4.1 Mixed effects modeling

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

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

819 regression. We compared models based on AIC. To account for variability between the studies

820 available from the Confidence Database20, mixed modeling was conducted using random

821 intercepts defined for each study. To account for variability across experimental session within

822 the IBL database21, mixed modeling was conducted using random intercepts defined for each

823 individual session. When multiple within-participant datapoints were analyzed, we estimated

824 random intercepts for each participant that were *nested* within the respective study of the

825 Confidence database20. By analogy, for the IBL database21, we estimated random intercepts

826 for each session that were nested within the respective mouse. We report *β* values referring

827 to the estimates provided by mixed effects modeling, followed by the respective T statistic

828 (linear models) or z statistic (logistic models).

829 The effects of stimulus- and history-congruence on RTs and confidence reports (Figure 2, 3

830 and 4, subpanels G-I) were assessed in linear mixed effects models that tested for main effects

831 of both stimulus- and history-congruence as well as the between-factor interaction. Thus, the

832 significance of any effect of history-congruence on RTs and confidence reports was assessed

833 while controlling for the respective effect of stimulus-congruence (and vice versa).

### 834 7.4.2 Psychometric function

835 We obtained psychometric curves by fitting the following error function to the behavioral

836 data:

*yp* = *γ* + (1 *− γ − δ*) *∗* (*erf* (

*sw* + *µ t*

) + 1)*/*2 (8)

837 We used the Broyden–Fletcher–Goldfarb–Shanno algorithm in maximum likelihood

838 estimation80 to predict individual choices *y* (outcome A: *y* = 0; outcome B: *y* = 1) from the

839 choice probability *yp*. In humans, we computed *sw* by multiplying the inputs *s* (stimulus A:

840 0; outcome B: 1) with the task difficulty *Db* (binarized across 7 levels):

*sw* = (*s −* 0*.*5) *∗ Db* (9)

841 In mice, *sw* was defined by the respective stimulus contrast in the two hemifields:

*sw* = *ContrastRight − ContrastLeft* (10)

842 Parameters of the psychometric error function were fitted using the R-package *optimx*80. The

843 psychometric error function was defined via the parameters *γ* (lower lapse; lower bound = 0,

844 upper bound = 0.5), *δ* (upper lapse; lower bound = 0, upper bound = 0.5), *µ* (bias; lower

845 bound humans = -5; upper bound humans = 5, lower bound mice = -0.5, upper bound mice

846 = 0.5) and threshold *t* (lower bound humans = 0.5, upper bound humans = 25; lower bound

847 mice = 0.01, upper bound mice = 1.5).

### 848 7.4.3 Computational modeling

849 **Model definition**: Our modeling analysis is an extension of a model proposed by Glaze et

850 al.51, who defined a normative account of evidence accumulation for decision-making. In this

851 model, trial-wise choices are explained by applying Bayes theorem to infer moment-by-moment

852 changes in the state of environment from trial-wise noisy observations across trials.

853 Following Glaze et al.51, we applied Bayes rule to compute the posterior evidence for the

854 two alternative choices (i.e., the log posterior ratio *L*) from the sensory evidence available at

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

856 respective precision terms *ωLLR* and *ωψ*:

*Lt* = *LLRt ∗ ωLLR* + *ψt*(*Lt−*1*, H*) *∗ ωψ* (11)

857 In the trial-wise design studied here, a transition between the two states of the environment

858 (i.e., the sources generating the noisy observations available to the participant) can occur

859 at any time. Despite the random nature of the psychophysical paradigms studied here20,21,

860 humans and mice showed significant biases toward preceding choices (Figure 2A and 3A).

861 We thus assumed that the prior probability of the two possible outcomes depends on the

862 posterior choice probability at the preceding trial and the hazard rate *H* assumed by the

863 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)

864 In this model, humans, mice and simulated agents make perceptual choices based on noisy

865 observations *u*. The are computed by applying a sensitivity parameter *α* to the content of

866 external sensory information *s*. For humans, we defined the input *s* by the two alternative

867 states of the environment (stimulus A: *s* = 0; stimulus B: *s* = 1), which generated the

868 observations *u* through a sigmoid function that applied a sensitivity parameter *α*:

*ut* = 1 + *exp*(*−α ∗* (*s*

1

*t*

*−* 0*.*5))

869 In mice, the inputs *s* were defined by the respective stimulus contrast in the two hemifields:

(13)

*st* = *ContrastRight − ContrastLeft* (14)

870 As in humans, we derived the input *u* by applying a sigmoid function with a sensitivity

871 parameter *α* to input *s*:

872

1

*ut*

= 1 + *exp*(*−α ∗ s* ) (15)

*t*

For humans, mice and in simulations, the log likelihood ratio *LLR* was computed from *u* as

873 follows:

*LLR* = *log*( *ut*

*t* 1

*− ut*

) (16)

874 To allow for long-range autocorrelation in stimulus- and history-congruence (Figure 2B and

875 3B), our modeling approach differed from Glaze et al.51 in that it allowed for systematic

876 fluctuation in the impact of sensory information (i.e., *LLR*) and the prior probability

877 of choices *ψ* on the posterior probability *L*. This was achieved by multiplying the log

878 likelihood ratio and the log prior ratio with coherent anti-phase fluctuations according to

879 *ωLLR* = *aLLR ∗ sin*(*f ∗ t* + *phase*) + 1 and *ωψ* = *aψ ∗ sin*(*f ∗ t* + *phase* + *π*) + 1.

880 **Model fitting**: In model fitting, we predicted the trial-wise choices *yt* (option A: 0; option B:

881 1) from inputs *s*. To this end, we minimized the log loss between *yt* and the choice probability

882 *ypt* in the unit interval. *ypt* was derived from *Lt* using a sigmoid function defined by the

883 inverse decision temperature *ζ*:

884

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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*

(lower bound = 1, upper bound = 10; human posterior = 4*.*63 ± 1*.*95 *×* 10*−*4; mouse posterior

894 = 4*.*82 ± 3*.*03 *×* 10*−*3) using maximum likelihood estimation with the Broyden–Fletcher–

895 Goldfarb–Shanno algorithm as implemented in the R-function *optimx*80 (see Supplemental

896 Table T2 for a description of our model parameters).

897 We validated the bimodal inference model in three steps: a formal model comparison to

898 reduced models based on AIC (Figure 1F-G; Supplemental Figure S9), the prediction of

899 within-training (stimulus- and history-congruence) as well as out-of-training variables (RT

900 and confidence), and a qualitative reproduction of the empirical data from model simulations

901 based on estimated parameters (Figure 4).

902 **Model comparison.** We assessed the following model space based on AIC:

903 • The full *bimodal inference model* (M1; Figure 1F) incorporates the influence of sensory

904 information according to the parameter *α* (likelihood); the integration of evidence across

905 trials according to the parameter *H* (prior); anti-phase oscillations in between likelihood

906 and prior precision according to *ωLLR* and *ωψ* with parameters *aLLR* (amplitude likelihood

907 fluctuation), *aψ* (amplitude prior fluctuation), *f* (frequency) and *p* (phase).

908 • The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the influence of sen-

909 sory information according to parameter *α* (likelihood); the integration of evidence across

910 trials according to parameter *H* (prior); oscillations in likelihood precision according

911 to *ωLLR* with parameters *aLLR* (amplitude likelihood fluctuation), *f* (frequency) and *p*

912 (phase).

913 • The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory

914 information according to parameter *α* (likelihood); the integration of evidence across

915 trials according to parameter *H* (prior); oscillations in the prior precision according

916 to *ωψ* with parameters *aψ* (amplitude prior fluctuation), *f* (frequency) and *p* (phase).

917 Please note that all models M1-3 lead to shifts in the relative precision of likelihood and

918 prior.

919 • The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the influence of

920 sensory information according to parameter *α* (likelihood); the integration of evidence

921 across trials according to parameter *H* (prior), There are no additional oscillations.

922 Model M4 thus corresponds to the model proposed by Glaze et al. and captures normative

923 evidence accumulation in unpredictable environments using a Bayesian update scheme51.

924 The comparison against M4 tests the null hypothesis that fluctuations in mode emerge

925 from a normative Bayesian model without the ad-hoc addition of oscillations as in models

926 M1-3.

927 • The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence of sensory

928 information according to parameter *α* (likelihood). The model lacks integration of

929 evidence across trials (flat prior) and oscillations. The comparison against M5 tests

930 the null hypothesis that observers do not use prior information derived from serial

931 dependency in perception.

932 **Prediction of within-training and out-of-training variables.** To validate our model, we

933 correlated individual posterior parameter estimates with the respective conventional variables.

934 As a sanity check, we tested (i), whether the estimated hazard rate *H* correlated negatively

935 with the frequency of history-congruent choices and, (ii), whether the estimated sensitivity to

936 sensory information *α* correlated positively with the frequency of stimulus-congruent choices.

937 In addition, we tested whether the posterior decision certainty (i.e.. the absolute of the log

938 posterior ratio) correlated negatively with RTs and positively with confidence. This allowed

939 us to assess whether our model could explain aspects of the data it was not fitted to (i.e.,

940 RTs and confidence).

941 **Simulations.** Finally, we used simulations (Figure 4, Supplemental Figures S10-13) to

942 show that all model components, including the anti-phase oscillations governed by *aψ*, *aLLR*,

943 *f* and *p*, were necessary for our model to reproduce the characteristics of the empirical

944 data. This enabled us to assess over- or under-fitting in the bimodal inference model and

945 all reduced models M2-M5. We used the posterior model parameters observed for humans

946 (*H*, *α*, *aψ*, *aLLR*, *f* , *p* and *ζ*) to define individual parameters for simulation in 4317 simulated

947 participants (i.e., equivalent to the number of human participants). For each participant, the

948 number of simulated trials was drawn at random between 300 to 700. Inputs *s* were drawn

949 at random for each trial, such that the sequence of inputs to the simulation did not contain

950 any systematic seriality. Noisy observations *u* were generated by applying the posterior

951 parameter *α* to inputs *s*, thus generating stimulus-congruent choices in 71*.*36 ± 2*.*6 *×* 10*−*3%

952 of trials. Choices were simulated based on the trial-wise choice probabilities *yp* obtained from

953 our model. Simulated data were analyzed in analogy to the human and mouse data. As a

954 substitute of subjective confidence, we computed the absolute of the trial-wise log posterior

955 ratio *|L|* (i.e., the posterior decision certainty).

956

957

# Figures

## Figure 1

959 **Figure 1. Concept.**

960 A. In binary perceptual decision-making, a participant is presented with stimuli from two

961 categories (A vs. B; dotted line) and reports consecutive perceptual choices via button presses

962 (sold line). All panels below refer to these stimulated example data.

963 B. When the response matches the external stimulus information (i.e., overlap between dotted

964 and solid line in panel A), perceptual choices are *stimulus-congruent* (red line). When the

965 response matches the response at the preceding trial, perceptual choices are *history-congruent*

966 (blue line).

967 C. The dynamic probabilities of stimulus- and history-congruence (i.e., computed in sliding

968 windows of ±5 trials) fluctuate over time.

969 D. The *mode* of perceptual processing is derived by computing the difference between the

970 dynamic probabilities of stimulus- and history-congruence. Values above 0% indicate a

971 bias toward external information, whereas values below 0% indicate a bias toward internal

972 information.

973 E. In computational modeling, internal mode is caused by an enhanced impact of perceptual

974 history. This causes the posterior (black line) to be close to the prior (blue line). Conversely,

975 during external mode, the posterior is close to the sensory information (log likelihood ratio,

976 red line).

977 F. The bimodal inference model (M1) explains fluctuations between externally- and externally-

978 biased modes (left panel) by two interacting factors: a normative accumulation of evidence

979 according to parameters *H* (middle panel), and anti-phase oscillations in the precision terms

980 *ωLLR* and *ωψ* (right panel).

981 G. The control models M2-M5 were constructed by successively removing the anti-phase

982 oscillations and the integration of information from the bimodal inference model. Please note

983 that the normative-evidence-accumulation-model (M4) corresponds to the model proposed

984 by Glaze et al.51. In the no-evidence-accumulation model (M5), perceptual decisions depend

985 only on likelihood information (flat priors).

986

## Figure 2

### 988 Figure 2. Internal and external modes in human perceptual decision-making.

989 A. In humans, perception was stimulus-congruent in 73.46% ± 0.15% (in red) and history-

990 congruent in 52.7% ± 0.12% of trials (in blue; upper panel). History-congruent perceptual

991 choices were more frequent when perception was stimulus-incongruent (i.e., on *error* trials;

992 lower panel), indicating that history effects impair performance in randomized psychophysical

993 designs.

994 B. Relative to randomly permuted data, we found highly significant autocorrelations of

995 stimulus-congruence and history-congruence (dots indicate intercepts *̸*= 0 in trial-wise linear

996 mixed effects modeling at p < 0.05). Across trials, the autocorrelation coefficients were best

997 fit by an exponential function (adjusted *R*2 for stimulus-congruence: 0.53; history-congruence:

998 0.72) as compared to a linear function (adjusted *R*2 for stimulus-congruence: 0.53; history-

999 congruence: 0.51), decaying at a rate of *γ* = *−*1*.*92 *×* 10*−*3 ± 4*.*5 *×* 10*−*4 (T(6*.*88 *×* 104)

|  |  |
| --- | --- |
| 1000 | = *−*4*.*27, p = 1*.*98 *×* 10*−*5) for stimulus-congruence and at a rate of *γ* = *−*6*.*11 *×* 10*−*3 ± |
| 1001 | 5*.*69 *×* 10*−*4 (T(6*.*75 *×* 104) = *−*10*.*74, p = 7*.*18 *×* 10*−*27) for history-congruence. |
| 1002 | C. Here, we depict the number of consecutive trials at which autocorrelation coefficients |
| 1003 | exceeded the respective autocorrelation of randomly permuted data within individual partici- |
| 1004 | pants. For stimulus-congruence (upper panel), the lag of positive autocorrelation amounted |
| 1005 | to 3*.*24 ± 2*.*39 *×* 10*−*3 on average, showing a peak at trial t+1 after the index trial. For |
| 1006 | history-congruence (lower panel), the lag of positive autocorrelation amounted to 4*.*87 ± |
| 1007 | 3*.*36 *×* 10*−*3 on average, peaking at trial t+2 after the index trial. |
| 1008 | D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ±5 |
| 1009 | trials) fluctuated as a scale-invariant process with a 1/f power law, i.e., at power densities |
| 1010 | that were inversely proportional to the frequency. |
| 1011 | E. The distribution of phase shift between fluctuations in stimulus- and history-congruence |
| 1012 | peaked at half a cycle (*π* denoted by dotted line). |
| 1013 | F. The average squared coherence between fluctuations in stimulus- and history-congruence |
| 1014 | (black dotted line) amounted to 6*.*49 ± 2*.*07 *×* 10*−*3% |
| 1015 | G. We observed faster RTs for both stimulus-congruence (as opposed to stimulus-incongruence, |
| 1016 | *β* = *−*0*.*14 ± 1*.*6 *×* 10*−*3, T(1*.*99 *×* 106) = *−*85*.*84, p < 2*.*2 *×* 10*−*308) and history-congruence |
| 1017 | (*β* = *−*9*.*56 *×* 10*−*3 ± 1*.*37 *×* 10*−*3, T(1*.*98 *×* 106) = *−*6*.*97, p = 3*.*15 *×* 10*−*12). |
| 1018 | H. The mode of perceptual processing (i.e., the difference between the smoothed probability |
| 1019 | of stimulus- vs. history-congruence) showed a quadratic relationship to RTs, with faster |
| 1020 | RTs for stronger biases toward both external sensory information and internal predictions |
| 1021 | provided by perceptual history (*β*2 = *−*19*.*86 ± 0*.*52, T(1*.*98 *×* 106) = *−*38*.*43, p = 5 *×* 10*−*323). |
| 1022 | The horizontal and vertical dotted lines indicate maximum RT and the associated mode, |
| 1023 | respectively. |
| 1024 | 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.

1031

## Figure 3

1033

### Figure 3. Internal and external modes in mouse perceptual decision-making.

|  |  |
| --- | --- |
| 1034 | A. In mice, 81.37% ± 0.3% of trials were stimulus-congruent (in red) and 54.03% ± 0.17% of |
| 1035 | trials were history-congruent (in blue; upper panel). History-congruent perceptual choices |
| 1036 | were not a consequence of the experimental design, but a source of error, as they were more |
| 1037 | frequent on stimulus-incongruent trials (lower panel). |
| 1038 | B. Relative to randomly permuted data, we found highly significant autocorrelations of |
| 1039 | stimulus-congruence and history-congruence (dots indicate intercepts *̸*= 0 in trial-wise linear |
| 1040 | mixed effects modeling at p < 0.05). Please note that the negative autocorrelation of |
| 1041 | stimulus-congruence at trial 2 was a consequence of the experimental design (Supplemental |
| 1042 | Figure 2D-F). As in humans, autocorrelation coefficients were best fit by an exponential |
| 1043 | function (adjusted *R*2 for stimulus-congruence: 0*.*44; history-congruence: 0*.*52) as compared |
| 1044 | to a linear function (adjusted *R*2 for stimulus-congruence: 3*.*16 *×* 10*−*3; history-congruence: |

|  |  |
| --- | --- |
| 1045 | 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) |
| 1046 | for stimulus-congruence and at a rate of *γ* = *−*6*.*7 *×* 10*−*3 ± 5*.*94 *×* 10*−*4 (T(3*.*69 *×* 104) = |
| 1047 | *−*11*.*27, p = 2*.*07 *×* 10*−*29) for history-congruence. |
| 1048 | C. For stimulus-congruence (upper panel), the lag of positive autocorrelation was longer in |
| 1049 | comparison to humans (4.59 ± 0.06 on average). For history-congruence (lower panel), the |
| 1050 | lag of positive autocorrelation was slightly shorter relative to humans (2.58 ± 0.01 on average, |
| 1051 | peaking at trial t+2 after the index trial). |
| 1052 | D. In mice, the dynamic probabilities of stimulus- and history-congruence (sliding windows |
| 1053 | of ±5 trials) fluctuated as a scale-invariant process with a 1/f power law. |
| 1054 | E. The distribution of phase shift between fluctuations in stimulus- and history-congruence |
| 1055 | peaked at half a cycle (*π* denoted by dotted line). |
| 1056 | F. The average squared coherence between fluctuations in stimulus- and history-congruence |
| 1057 | (black dotted line) amounted to 3.45 ± 0.01%. |
| 1058 | G. We observed shorter trial durations (TDs) for stimulus-congruence (as opposed to stimulus- |
| 1059 | incongruence, *β* = *−*1*.*12 ± 8*.*53 *×* 10*−*3, T(1*.*34 *×* 106) = *−*131*.*78, p < 2*.*2 *×* 10*−*308), but |
| 1060 | longer TDs for history-congruence (*β* = 0*.*06 ± 6*.*76 *×* 10*−*3, T(1*.*34 *×* 106) = 8*.*52, p = |
| 1061 | 1*.*58 *×* 10*−*17). |
| 1062 | H. TDs decreased monotonically for stronger biases toward external mode (*β*1 = *−*4*.*16 *×* 104 |
| 1063 | ± 1*.*29 *×* 103, T(1*.*35 *×* 106) = *−*32*.*31, p = 6*.*03 *×* 10*−*229). The horizontal and vertical dotted |
| 1064 | lines indicate maximum TD and the associated mode, respectively. |
| 1065 | I. For TDs that differed from the median TD by no more than 1.5 x MAD (median absolute |
| 1066 | distance49), mice exhibited a quadratic component in the relationship between the mode of |
| 1067 | sensory processing and TDs (*β*2 = *−*1*.*97 *×* 103 ± 843*.*74, T(1*.*19 *×* 106) = *−*2*.*34, p = 0*.*02). |
| 1068 | This explorative post-hoc analysis focuses on trials at which mice engage more swiftly with |
| 1069 | 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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| 1074 | A. Simulated perceptual choices were stimulus-congruent in 71.36% ± 0.17% (in red) and |
| 1075 | history-congruent in 51.99% ± 0.11% of trials (in blue; T(4*.*32*×*103) = 17*.*42, p = 9*.*89*×*10*−*66; |
| 1076 | upper panel). Due to the competition between stimulus- and history-congruence, history- |
| 1077 | congruent perceptual choices were more frequent when perception was stimulus-incongruent |
| 1078 | (i.e., on *error* trials; T(4*.*32 *×* 103) = 11.19, p = 1*.*17 *×* 10*−*28; lower panel) and thus impaired |
| 1079 | performance in the randomized psychophysical design simulated here. |
| 1080 | B. At the simulated group level, we found significant autocorrelations in both stimulus- |
| 1081 | congruence (13 consecutive trials) and history-congruence (30 consecutive trials). |
| 1082 | C. On the level of individual simulated participants, autocorrelation coefficients exceeded the |
| 1083 | autocorrelation coefficients of randomly permuted data within a lag of 2*.*46 ± 1*.*17 *×* 10*−*3 |

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| 1084 | trials for stimulus-congruence and 4*.*24 ± 1*.*85 *×* 10*−*3 trials for history-congruence. |
| 1085 | D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ±5 |
| 1086 | trials) fluctuated as a scale-invariant process with a 1/f power law, i.e., at power densities |
| 1087 | that were inversely proportional to the frequency (power ~ 1/*fβ*; stimulus-congruence: *β* = |
| 1088 | *−*0*.*81 ± 1*.*18 *×* 10*−*3, T(1*.*92 *×* 105) = *−*687*.*58, p < 2*.*2 *×* 10*−*308; history-congruence: *β* = |
| 1089 | *−*0*.*83 ± 1*.*27 *×* 10*−*3, T(1*.*92 *×* 105) = *−*652*.*11, p < 2*.*2 *×* 10*−*308). |
| 1090 | E. The distribution of phase shift between fluctuations in simulated stimulus- and history- |
| 1091 | congruence peaked at half a cycle (*π* denoted by dotted line). The dynamic probabilities of |
| 1092 | simulated stimulus- and history-congruence were therefore were strongly anti-correlated (*β* = |
| 1093 | *−*0*.*03 ± 8*.*22 *×* 10*−*4, T(2*.*12 *×* 106) = *−*40*.*52, p < 2*.*2 *×* 10*−*308). |
| 1094 | F. The average squared coherence between fluctuations in simulated stimulus- and history- |
| 1095 | congruence (black dotted line) amounted to 6*.*49 ± 2*.*07 *×* 10*−*3%. |
| 1096 | G. Simulated confidence was enhanced for stimulus-congruence (*β* = 0*.*03 ± 1*.*71 *×* 10*−*4, |
| 1097 | T(2*.*03 *×* 106) = 178*.*39, p < 2*.*2 *×* 10*−*308) and history-congruence (*β* = 0*.*01 ± 1*.*5 *×* 10*−*4, |
| 1098 | T(2*.*03 *×* 106) = 74*.*18, p < 2*.*2 *×* 10*−*308). |
| 1099 | H. In analogy to humans, the simulated data showed a quadratic relationship between the |
| 1100 | mode of perceptual processing and posterior certainty, which increased for stronger external |
| 1101 | and internal biases (*β*2 = 31*.*03 ± 0*.*15, T(2*.*04 *×* 106) = 205*.*95, p < 2*.*2 *×* 10*−*308). The |
| 1102 | horizontal and vertical dotted lines indicate minimum posterior certainty and the associated |
| 1103 | 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