

# 1 Title Page

## Bimodal Inference in Humans and Mice

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## <sup>1</sup> 2 Abstract

<sup>2</sup> Perception is known to cycle through periods of enhanced and reduced sensitivity to external  
<sup>3</sup> information. Here, we asked whether such slow fluctuations arise as a noise-related epiphe-  
<sup>4</sup> nomenon of limited processing capacity or, alternatively, represent a structured mechanism  
<sup>5</sup> of perceptual inference. Using two large-scale datasets, we found that humans and mice  
<sup>6</sup> alternate between externally- and internally-oriented modes of sensory analysis. During  
<sup>7</sup> external mode, perception aligns more closely with the external sensory information, whereas  
<sup>8</sup> internal mode is characterized by enhanced biases toward perceptual history. Computational  
<sup>9</sup> modeling indicated that dynamic changes in mode are enabled by two interlinked factors:  
<sup>10</sup> (i), the integration of subsequent inputs over time and, (ii), slow anti-phase oscillations  
<sup>11</sup> in the perceptual impact of external sensory information versus internal predictions that  
<sup>12</sup> are provided by perceptual history. We propose that between-mode fluctuations generate  
<sup>13</sup> unambiguous error signals that enable optimal inference in volatile environments.

## <sup>14</sup> 3 One sentence summary

<sup>15</sup> Humans and mice fluctuate between external and internal modes of sensory processing.

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<sup>18</sup> **4 Introduction**

<sup>19</sup> The capacity to respond to changes in the environment is a defining feature of life<sup>1–3</sup>.  
<sup>20</sup> Intriguingly, the ability of living things to process their surroundings fluctuates considerably  
<sup>21</sup> over time<sup>4,5</sup>. In humans and mice, perception<sup>6–12</sup>, cognition<sup>13</sup> and memory<sup>14</sup> cycle through  
<sup>22</sup> prolonged periods of enhanced and reduced sensitivity to external information, suggesting  
<sup>23</sup> that the brain detaches from the world in recurring intervals that last from milliseconds to  
<sup>24</sup> seconds and even minutes<sup>4</sup>. Yet breaking from external information is risky, as swift responses  
<sup>25</sup> to the environment are often crucial to survival.

<sup>26</sup> What could be the reason for these fluctuations in perceptual performance<sup>11</sup>? First, periodic  
<sup>27</sup> fluctuations in the ability to parse external information<sup>11,15,16</sup> may arise simply due to  
<sup>28</sup> bandwidth limitations and noise. Second, it may be advantageous to actively reduce the costs  
<sup>29</sup> of neural processing by seeking sensory information only in recurring intervals<sup>17</sup>, otherwise  
<sup>30</sup> relying on random or stereotypical responses to the external world. Third, spending time away  
<sup>31</sup> from the ongoing stream of sensory inputs may also reflect a functional strategy that facilitates  
<sup>32</sup> flexible behavior and learning<sup>18</sup>: Intermittently relying more strongly on information acquired  
<sup>33</sup> from past experiences may enable agents to build up stable internal predictions about the  
<sup>34</sup> environment despite an ongoing stream of external sensory signals<sup>19</sup>. By the same token,  
<sup>35</sup> recurring intervals of enhanced sensitivity to external information may help to detect changes  
<sup>36</sup> in both the state of the environment and the amount of noise that is inherent in sensory  
<sup>37</sup> encoding<sup>19</sup>.

<sup>38</sup> In this work, we sought to elucidate whether periodicities in the sensitivity to external  
<sup>39</sup> information represent an epiphenomenon of limited processing capacity or, alternatively,  
<sup>40</sup> result from a structured and adaptive mechanism of perceptual inference. To this end, we  
<sup>41</sup> analyzed two large-scale datasets on perceptual decision-making in humans<sup>20</sup> and mice<sup>21</sup>.  
<sup>42</sup> When less sensitive to external stimulus information, humans and mice did not behave more  
<sup>43</sup> randomly, but showed stronger serial dependencies in their perceptual choices<sup>22–33</sup>. These

<sup>44</sup> serial dependencies may be understood as driven by internal predictions that reflect the auto-  
<sup>45</sup> correlation of natural environments<sup>34</sup> and bias perception toward preceding experiences<sup>30,31,35</sup>.  
<sup>46</sup> Computational modeling indicated that ongoing changes in perceptual performance may  
<sup>47</sup> be driven by systematic fluctuations between externally- and internally-oriented *modes* of  
<sup>48</sup> sensory analysis. We suggest that such *bimodal inference* may help to build stable internal  
<sup>49</sup> representations of the sensory environment despite an ongoing stream of sensory information.

## <sup>50</sup> 5 Results

### <sup>51</sup> 5.1 Human perception fluctuates between epochs of enhanced and <sup>52</sup> reduced sensitivity to external information

<sup>53</sup> We began by selecting 66 studies from the Confidence Database<sup>20</sup> that investigated how  
<sup>54</sup> human participants ( $N = 4317$ ) perform binary perceptual decisions (Figure 1A; see Methods  
<sup>55</sup> for details on inclusion criteria). As a metric for perceptual performance (i.e., the sensitivity  
<sup>56</sup> to external sensory information), we asked whether the participant's response and the  
<sup>57</sup> presented stimulus matched (*stimulus-congruent* choices) or differed from each other (*stimulus-*  
<sup>58</sup> *incongruent* choices; Figure 1B and C) in a total of 21.05 million trials.

<sup>59</sup> In a first step, we asked whether the ability to accurately perceive sensory stimuli is constant  
<sup>60</sup> over time or, alternatively, fluctuates in periods of enhanced and reduced sensitivity to  
<sup>61</sup> external information. We found perception to be stimulus-congruent in  $73.46\% \pm 0.15\%$  of  
<sup>62</sup> trials (mean  $\pm$  standard error of the mean; Figure 2A), which was highly consistent across  
<sup>63</sup> the selected studies (Supplemental Figure S1A). In line with previous work<sup>8</sup>, we found that  
<sup>64</sup> the probability of stimulus-congruence was not independent across successive trials: At the  
<sup>65</sup> group level, stimulus-congruent perceptual choices were significantly autocorrelated for up  
<sup>66</sup> to 15 trials (Figure 2B), controlling for task difficulty and the sequence of presented stimuli  
<sup>67</sup> (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  $3.24 \pm 2.39 \times 10^{-3}$   
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 information<sup>8</sup>.  
79 As a consequence of this autocorrelation, the dynamic probability of stimulus-congruent  
80 perception (i.e., computed in sliding windows of  $\pm 5$  trials; Figure 1C) fluctuated considerably  
81 within participants (average minimum:  $35.46\% \pm 0.22\%$ , maximum:  $98.27\% \pm 0.07\%$ ). In  
82 line with previous findings<sup>9</sup>, such fluctuations in the sensitivity to external information had  
83 a power density that was inversely proportional to the frequency in the slow spectrum<sup>11</sup>  
84 ( $\text{power} \sim 1/f^\beta$ ,  $\beta = -1.32 \pm 3.14 \times 10^{-3}$ ,  $T(1.84 \times 10^5) = -419.48$ ,  $p < 2.2 \times 10^{-308}$ ; Figure  
85 2D). This feature, which is also known as a *1/f power law*<sup>36,37</sup>, represents a characteristic  
86 of scale-free fluctuations in complex dynamic systems such as the brain<sup>38</sup> and the cognitive  
87 processes it entertains<sup>9,10,13,39,40</sup>.

## 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 information<sup>4</sup>. 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 experiences<sup>19,31</sup>.

94 In perception, *serial dependencies* represent one of the most basic internal predictions that  
95 cause perceptual decisions to be systematically biased toward preceding choices<sup>22–33</sup>. Such  
96 effects of perceptual history mirror the continuity of the external world, in which the recent  
97 past often predicts the near future<sup>30,31,34,35,41</sup>. 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  $52.7\% \pm 0.12\%$  history-  
103 congruent trials, we found a small but highly significant perceptual bias towards preceding  
104 experiences ( $\beta = 16.18 \pm 1.07$ ,  $T(1.09 \times 10^3) = 15.07$ ,  $p = 10^{-46}$ ; 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 ( $56.03\% \pm 0.2\%$ ) as opposed to stimulus-congruent ( $51.77\% \pm 0.11\%$ ,  $\beta = -4.26 \pm 0.21$ ,  
110  $T(8.57 \times 10^3) = -20.36$ ,  $p = 5.28 \times 10^{-90}$ ; Figure 2A, lower panel). Despite being adaptive in  
111 autocorrelated real-world environments<sup>19,34,35,42</sup>, perceptual history thus represented a source  
112 of bias in the randomized experimental designs studied here<sup>24,28,30,31,43</sup>. 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 9.1).

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

<sup>119</sup> to 21 trials (Figure 2B), while controlling for task difficulty and the sequence of presented  
<sup>120</sup> stimuli (Supplemental Figure 2A-B). In individual participants, the autocorrelation of history-  
<sup>121</sup> congruence was elevated above randomly permuted data for a lag of  $4.87 \pm 3.36 \times 10^{-3}$   
<sup>122</sup> trials (Figure 2C), confirming that the autocorrelation of history-congruence was not only  
<sup>123</sup> a group-level phenomenon. The autocorrelation of history-congruence was corroborated by  
<sup>124</sup> logistic regression models that successfully predicted the history-congruence of perception at  
<sup>125</sup> an index trial  $t = 0$  from the history-congruence at the preceding trials within a lag of 17  
<sup>126</sup> trials (Supplemental Figure S3).

<sup>127</sup> Third, we asked whether the impact of internal information fluctuates as a scale-invariant  
<sup>128</sup> process with a 1/f power law (i.e., the feature typically associated with fluctuations in the  
<sup>129</sup> sensitivity to external information<sup>9,10,13,39,40</sup>). The dynamic probability of history-congruent  
<sup>130</sup> perception (i.e., computed in sliding windows of  $\pm 5$  trials; Figure 1C) varied considerably  
<sup>131</sup> over time, ranging between a minimum of  $12.77\% \pm 0.14\%$  and a maximum  $92.23\% \pm 0.14\%$ .  
<sup>132</sup> In analogy to stimulus-congruence, we found that history-congruence fluctuated as at power  
<sup>133</sup> densities that were inversely proportional to the frequency in the slow spectrum<sup>11</sup> (power  $\sim$   
<sup>134</sup>  $1/f^\beta$ ,  $\beta = -1.34 \pm 3.16 \times 10^{-3}$ ,  $T(1.84 \times 10^5) = -423.91$ ,  $p < 2.2 \times 10^{-308}$ ; Figure 2D).

<sup>135</sup> Finally, we ensured that fluctuations in stimulus- and history-congruence are linked to each  
<sup>136</sup> other. When perceptual choices were less biased toward external information, participants  
<sup>137</sup> relied more strongly on internal information acquired from perceptual history (and vice  
<sup>138</sup> versa,  $\beta = -0.05 \pm 5.63 \times 10^{-4}$ ,  $T(2.1 \times 10^6) = -84.21$ ,  $p < 2.2 \times 10^{-308}$ , controlling for  
<sup>139</sup> fluctuations in general response biases; Supplemental Section 9.2). Thus, while sharing the  
<sup>140</sup> 1/f power law characteristic, fluctuations in stimulus- and history-congruence were shifted  
<sup>141</sup> against each other by approximately half a cycle and showed a squared coherence of  $6.49 \pm$   
<sup>142</sup>  $2.07 \times 10^{-3}\%$  (Figure 2E and F; we report the average phase and coherence for frequencies  
<sup>143</sup> below  $0.1 / N_{trials}$ ; see Methods for details).

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

<sup>145</sup> external sensory signals with internal predictions provided by perceptual history. We show  
<sup>146</sup> that the impact of these external and internal sources of information is not stable over time,  
<sup>147</sup> but fluctuates systematically, emitting overlapping autocorrelation curves and antiphase 1/f  
<sup>148</sup> profiles.

<sup>149</sup> These links between stimulus- and history-congruence suggest that the fluctuations in the  
<sup>150</sup> impact of external and internal information may be generated by a unifying mechanism that  
<sup>151</sup> causes perception to alternate between two opposing *modes*<sup>18</sup> (Figure 1D): During *external*  
<sup>152</sup> *mode*, perception is more strongly driven by the available external stimulus information.  
<sup>153</sup> Conversely, during *internal mode*, participants rely more heavily on internal predictions  
<sup>154</sup> that are implicitly provided by preceding perceptual experiences. The fluctuations in the  
<sup>155</sup> degree of bias toward external versus internal information created by such *bimodal inference*  
<sup>156</sup> may thus provide a novel explanation for ongoing fluctuations in the sensitivity to external  
<sup>157</sup> information<sup>4,5,18</sup>.

### <sup>158</sup> **5.3 Internal and external modes of processing facilitate response 159 behavior and enhance confidence in human perceptual decision- 160 making**

<sup>161</sup> The above results point to systematic fluctuations in the *decision variable*<sup>44</sup> that determines  
<sup>162</sup> perceptual choices, causing enhanced sensitivity to external stimulus information during  
<sup>163</sup> external mode and increased biases toward preceding choices during internal mode. As such,  
<sup>164</sup> fluctuations in mode should influence downstream aspects of behavior and cognition that  
<sup>165</sup> operate on the perceptual decision variable<sup>44</sup>. To test this hypothesis with respect to motor  
<sup>166</sup> behavior and metacognition, we asked how bimodal inference relates to response times (RTs)  
<sup>167</sup> and confidence reports.

<sup>168</sup> With respect to RTs, we observed faster responses for stimulus-congruent as opposed to  
<sup>169</sup> stimulus-incongruent choices ( $\beta = -0.14 \pm 1.6 \times 10^{-3}$ ,  $T(1.99 \times 10^6) = -85.84$ ,  $p < 2.2 \times 10^{-308}$ ;

<sup>170</sup> Figure 2G). Intriguingly, whilst controlling for the effect of stimulus-congruence, we found  
<sup>171</sup> that history-congruent (as opposed to history-incongruent) choices were also characterized by  
<sup>172</sup> faster responses ( $\beta = -9.56 \times 10^{-3} \pm 1.37 \times 10^{-3}$ ,  $T(1.98 \times 10^6) = -6.97$ ,  $p = 3.15 \times 10^{-12}$ ;  
<sup>173</sup> Figure 2G).

<sup>174</sup> When analyzing the speed of response against the mode of sensory processing (Figure 2H),  
<sup>175</sup> we found that RTs were shorter during externally-oriented perception ( $\beta_1 = -11.07 \pm 0.55$ ,  
<sup>176</sup>  $T(1.98 \times 10^6) = -20.14$ ,  $p = 3.17 \times 10^{-90}$ ). Crucially, as indicated by a quadratic relationship  
<sup>177</sup> between the mode of sensory processing and RTs ( $\beta_2 = -19.86 \pm 0.52$ ,  $T(1.98 \times 10^6) =$   
<sup>178</sup>  $-38.43$ ,  $p = 5 \times 10^{-323}$ ), participants became faster at indicating their perceptual decision  
<sup>179</sup> when biases toward both internal and external mode grew stronger.

<sup>180</sup> In analogy to the speed of response, confidence was higher for stimulus-congruent as opposed  
<sup>181</sup> to stimulus-incongruent choices ( $\beta = 0.04 \pm 1.18 \times 10^{-3}$ ,  $T(2.06 \times 10^6) = 36.85$ ,  $p =$   
<sup>182</sup>  $3.25 \times 10^{-297}$ ; Figure 2I). Yet whilst controlling for the effect of stimulus-congruence, we found  
<sup>183</sup> that history-congruence also increased confidence ( $\beta = 0.48 \pm 1.38 \times 10^{-3}$ ,  $T(2.06 \times 10^6) =$   
<sup>184</sup>  $351.54$ ,  $p < 2.2 \times 10^{-308}$ ; Figure 2I).

<sup>185</sup> When depicted against the mode of sensory processing (Figure 2J), subjective confidence was  
<sup>186</sup> indeed enhanced when perception was more externally-oriented ( $\beta_1 = 92.63 \pm 1$ ,  $T(2.06 \times 10^6)$   
<sup>187</sup>  $= 92.89$ ,  $p < 2.2 \times 10^{-308}$ ). Importantly, however, participants were more confident in their  
<sup>188</sup> perceptual decision for stronger biases toward both internal and external mode ( $\beta_2 = 39.3 \pm$   
<sup>189</sup>  $0.94$ ,  $T(2.06 \times 10^6) = 41.95$ ,  $p < 2.2 \times 10^{-308}$ ). In analogy to RTs, subjective confidence thus  
<sup>190</sup> showed a quadratic relationship to the mode of sensory processing (Figure 2J).

<sup>191</sup> Consequently, our findings predict that human participants lack full metacognitive insight  
<sup>192</sup> into how strongly external signals and internal predictions contribute to perceptual decision-  
<sup>193</sup> making. Stronger biases toward perceptual history thus lead to two seemingly contradictory  
<sup>194</sup> effects, more frequent errors (Supplemental Figure 1C) and increasing subjective confidence  
<sup>195</sup> (Figure 2I-J). This observation generates an intriguing prediction regarding the association of

<sup>196</sup> between-mode fluctuations and perceptual metacognition: Metacognitive efficiency should be  
<sup>197</sup> lower in individuals who spend more time in internal mode, since their confidence reports are  
<sup>198</sup> less predictive of whether the corresponding perceptual decision is correct. We computed each  
<sup>199</sup> participant's M-ratio<sup>45</sup> ( $\text{meta-d}'/\text{d}' = 0.85 \pm 0.02$ ) to probe this hypothesis independently  
<sup>200</sup> of inter-individual differences in perceptual performance. Indeed, we found that biases  
<sup>201</sup> toward internal information (as defined by the average probability of history-congruence) were  
<sup>202</sup> stronger in participants with lower metacognitive efficiency ( $\beta = -2.98 \times 10^{-3} \pm 9.82 \times 10^{-4}$ ,  
<sup>203</sup>  $T(4.14 \times 10^3) = -3.03$ ,  $p = 2.43 \times 10^{-3}$ ).

<sup>204</sup> In sum, the above results indicate that reporting behavior and metacognition do not map  
<sup>205</sup> linearly onto the mode of sensory processing. Rather, they suggest that slow fluctuations in the  
<sup>206</sup> respective impact of external and internal information are most likely to affect perception at  
<sup>207</sup> an early level of sensory analysis<sup>46,47</sup>. Such low-level processing may thus integrate perceptual  
<sup>208</sup> history with external inputs into a decision variable<sup>44</sup> that influences not only perceptual  
<sup>209</sup> choices, but also the speed and confidence at which they are made.

<sup>210</sup> In what follows, we probe alternative explanations for between-mode fluctuations, test for  
<sup>211</sup> the existence of modes in mice, and propose a predictive processing model that explains  
<sup>212</sup> fluctuations in mode ongoing shifts in the precision afforded to external sensory information  
<sup>213</sup> relative to internal predictions driven by perceptual history.

#### <sup>214</sup> **5.4 Fluctuations between internal and external mode cannot be 215 reduced to general response biases or random choices**

<sup>216</sup> The core assumption of bimodal inference - that ongoing changes in the sensitivity to external  
<sup>217</sup> information are driven by internal predictions induced via perceptual history - needs to  
<sup>218</sup> be contrasted against two alternative hypotheses: When making errors, observers may not  
<sup>219</sup> engage with the task and respond stereotypically, i.e., exhibit stronger general biases toward  
<sup>220</sup> one of the two potential outcomes, or simply choose randomly.

<sup>221</sup> Logistic regression confirmed that perceptual history made a significant contribution to  
<sup>222</sup> perception ( $\beta = 0.11 \pm 5.79 \times 10^{-3}$ ,  $z = 18.53$ ,  $p = 1.1 \times 10^{-76}$ ) over and above the ongoing  
<sup>223</sup> stream of external sensory information ( $\beta = 2.2 \pm 5.87 \times 10^{-3}$ ,  $z = 375.11$ ,  $p < 2.2 \times 10^{-308}$ )  
<sup>224</sup> and general response biases toward ( $\beta = 15.19 \pm 0.08$ ,  $z = 184.98$ ,  $p < 2.2 \times 10^{-308}$ ).

<sup>225</sup> When eliminating perceptual history as a predictor of individual choices at individual trials,  
<sup>226</sup> Akaike Information Criterion (AIC<sup>48</sup>) increased by  $\delta_{AIC} = 1.64 \times 10^3$  (see Supplemental  
<sup>227</sup> Figure S4A-B for parameter- and model-level inference at the level of individual observers).  
<sup>228</sup> Likewise, when eliminating slow fluctuations in history-congruence as a predictor of slow  
<sup>229</sup> fluctuations in stimulus-congruence across trials, we observed an increase in AIC by  $\delta_{AIC}$   
<sup>230</sup> =  $7.06 \times 10^3$ . These results provided model-level evidence against the null hypotheses that  
<sup>231</sup> fluctuations in stimulus-congruence are driven exclusively by choice randomness or general  
<sup>232</sup> response bias (see Supplemental Section 9.2 and Supplemental Figure S5 for an in-depth  
<sup>233</sup> assessment of general response bias).

<sup>234</sup> To confirm that changes in the sensitivity to external information are indicative of internal  
<sup>235</sup> mode processing, we estimated full and history-dependent psychometric curves during internal,  
<sup>236</sup> external, and across modes<sup>21</sup>. If, as we hypothesized, internal mode processing reflects an  
<sup>237</sup> enhanced impact of perceptual history, one would expect a history-dependent increase in  
<sup>238</sup> biases and lapses as well as a history-independent increase in threshold. Conversely, if internal  
<sup>239</sup> mode processing were driven by random choices, one would expect a history-independent  
<sup>240</sup> increase in lapses and threshold, and no change in bias. In line with our prediction, we found  
<sup>241</sup> that internal mode processing was associated with a history-dependent increase in bias and  
<sup>242</sup> lapse as well as a history-independent increase in threshold (Supplemental Section 9.3.1 and  
<sup>243</sup> Supplemental Figure S6). This confirmed that internal mode processing is indeed driven by  
<sup>244</sup> an enhanced impact of perceptual history.

<sup>245</sup> In line with this, the quadratic relationship between mode and confidence (Figure 2J)  
<sup>246</sup> 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 9.4.1).

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 dependencies<sup>22–28,32,33,46</sup>, perceptual history  
258 is cast as an internal prediction that leverages the temporal autocorrelation of natural  
259 environments for efficient decision-making<sup>30,31,34,35,41</sup>. 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) dataset<sup>21</sup>. We restricted our analyses to the  
265 *basic task*<sup>21</sup>, 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  $81.37\% \pm 0.3\%$  of trials (Figure 3A, upper  
271 panel). In line with humans, mice were biased toward perceptual history in  $54.03\% \pm 0.17\%$

272 of trials ( $T(164) = 23.65$ ,  $p = 9.98 \times 10^{-55}$ ; 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 hemifield<sup>21</sup>, 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 ( $61.59\% \pm 0.07\%$ ) as opposed to stimulus-congruent ( $51.81\% \pm 0.02\%$ ,  
277  $T(164) = 31.37$ ,  $p = 3.36 \times 10^{-71}$ ;  $T(164) = 31.37$ ,  $p = 3.36 \times 10^{-71}$ ; Figure 3A, lower panel),  
278 confirming that perceptual history was a source of bias<sup>24,28,30,31,43</sup> 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 stimuli<sup>21</sup>.

288 At the level of individual mice, autocorrelation coefficients were elevated above randomly  
289 permuted data within a lag of  $4.59 \pm 0.06$  trials for stimulus-congruence and  $2.58 \pm 0.01$   
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 variable<sup>44</sup> that determines not only perceptual choices, but also down-  
300 stream aspects of mouse behavior<sup>44</sup>. 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 feedback<sup>21</sup>). Stimulus-congruent (as opposed to stimulus-incongruent)  
303 choices were associated with shorter TDs ( $\delta = -262.48 \pm 17.1$ ,  $T(164) = -15.35$ ,  $p =$   
304  $1.55 \times 10^{-33}$ ), while history-congruent choices were characterized by longer TDs ( $\delta = 30.47$   
305  $\pm 5.57$ ,  $T(164) = 5.47$ ,  $p = 1.66 \times 10^{-7}$ ; 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 ( $\beta_1 = -4.16 \times 10^4 \pm$   
308  $1.29 \times 10^3$ ,  $T(1.35 \times 10^6) = -32.31$ ,  $p = 6.03 \times 10^{-229}$ , Figure 3H). However, an explorative  
309 post-hoc analysis limited to TDs that differed from the median TD by no more than  $1.5 \times$   
310 MAD (median absolute distance<sup>49</sup>) 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 ( $\beta_2 = -1.97 \times 10^3 \pm 843.74$ ,  $T(1.19 \times 10^6) = -2.34$ ,  $p = 0.02$ , 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 ( $\beta = 0.51 \pm 4.49 \times 10^{-3}$ ,  $z = 112.84$ ,  $p < 2.2 \times 10^{-308}$ ), while controlling  
317 for external sensory information ( $\beta = 2.96 \pm 4.58 \times 10^{-3}$ ,  $z = 646.1$ ,  $p < 2.2 \times 10^{-308}$ ) and  
318 general response biases toward one of the two outcomes ( $\beta = -1.78 \pm 0.02$ ,  $z = -80.64$ ,  $p$   
319  $< 2.2 \times 10^{-308}$ ). When eliminating perceptual history as a predictor of individual choices,  
320 AIC increased by  $\delta_{AIC} = 1.48 \times 10^4$ , 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

<sup>324</sup> stimulus-congruence ( $\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$ ,  $T(1.34 \times 10^6) = -168.39$ ,  $p < 2.2 \times 10^{-308}$ )  
<sup>325</sup> beyond the effect of ongoing changes in general response biases ( $\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$ ,  
<sup>326</sup>  $T(1.34 \times 10^6) = -48.14$ ,  $p < 2.2 \times 10^{-308}$ ). Eliminating the dynamic fluctuations in history-  
<sup>327</sup> congruence as a predictor of fluctuations in stimulus-congruence resulted in an increase in  
<sup>328</sup> AIC by  $\delta_{AIC} = 2.8 \times 10^4$  (see Supplemental Section 9.2 and Supplemental Figure S5 for an  
<sup>329</sup> in-depth assessment of general response bias).

<sup>330</sup> When fitting full and history-conditioned psychometric curves to the IBL data<sup>21</sup>, we observed  
<sup>331</sup> that internal mode processing was associated with a history-dependent increase in bias and  
<sup>332</sup> lapse as well as a history-independent increase in threshold (Supplemental Section 9.3.2 and  
<sup>333</sup> Supplemental Figure S7). Over time, the frequency of history-congruent choices increased  
<sup>334</sup> alongside stimulus-congruence and speed of response as mice were exposed to the experiment,  
<sup>335</sup> arguing against the proposition that biases toward perceptual history reflected an unspecific  
<sup>336</sup> response strategy in mice who were not sufficiently trained on the IBL task (Supplemental  
<sup>337</sup> Section 9.4.2 and Supplemental Figure S8).

<sup>338</sup> In sum, these analyses confirmed that the observed fluctuations in sensitivity to external  
<sup>339</sup> sensory information are driven by dynamic changes in impact of perceptual history and  
<sup>340</sup> cannot be reduced to general response bias and random choice behavior.

## <sup>341</sup> **5.6 Fluctuations in mode result from coordinated changes in the 342 impact of external and internal information on perception**

<sup>343</sup> The empirical data presented above indicate that, for both humans and mice, perception  
<sup>344</sup> fluctuates between external and modes, i.e., multi-trial epochs that are characterized by  
<sup>345</sup> enhanced sensitivity toward either external sensory information or internal predictions  
<sup>346</sup> generated by perceptual history. Since natural environments typically show high temporal  
<sup>347</sup> redundancy<sup>34</sup>, previous experiences are often good predictors of new stimuli<sup>30,31,35,41</sup>. Serial  
<sup>348</sup> dependencies may therefore induce autocorrelations in perception by serving as internal

<sup>349</sup> predictions (or *memory* processes<sup>9,13</sup>) that actively integrate noisy sensory information over  
<sup>350</sup> time<sup>50</sup>.

<sup>351</sup> Previous work has shown that such internal predictions can be built by dynamically updating  
<sup>352</sup> the estimated probability of being in a particular perceptual state from the sequence of  
<sup>353</sup> preceding experiences<sup>35,46,51</sup>. The integration of sequential inputs may lead to accumulating  
<sup>354</sup> effects of perceptual history that progressively override incoming sensory information, enabling  
<sup>355</sup> internal mode processing<sup>19</sup>. However, since such a process would lead to internal biases that  
<sup>356</sup> may eventually become impossible to overcome<sup>52</sup>, changes in mode may require ongoing  
<sup>357</sup> wave-like fluctuations<sup>9,13</sup> in the perceptual impact of external and internal information that  
<sup>358</sup> occur *irrespective* of the sequence of previous experiences and temporarily de-couple the  
<sup>359</sup> decision variable from implicit internal representations of the environment<sup>19</sup>.

<sup>360</sup> Following Bayes' theorem, binary perceptual decisions depend on the log posterior ratio  $L$  of  
<sup>361</sup> the two alternative states of the environment that participants learn about via noisy sensory  
<sup>362</sup> information<sup>51</sup>. We computed the posterior by combining the sensory evidence available at  
<sup>363</sup> time-point  $t$  (i.e., the log likelihood ratio  $LLR$ ) with the prior probability  $\psi$ , weighted by the  
<sup>364</sup> respective precision terms  $\omega_{LLR}$  and  $\omega_\psi$ :

$$L_t = LLR_t * \omega_{LLR} + \psi_t(L_{t-1}, H) * \omega_\psi \quad (1)$$

<sup>365</sup> We derived the prior probability  $\psi$  at timepoint  $t$  from the posterior probability of perceptual  
<sup>366</sup> outcomes at timepoint  $L_{t-1}$ . Since a switch between the two states can occur at any time,  
<sup>367</sup> the effect of perceptual history varies according to both the sequence of preceding experiences  
<sup>368</sup> and the estimated stability of the external environment (i.e., the *hazard rate*  $H^{51}$ ):

$$\psi_t(L_{t-1}, H) = L_{t-1} + \log\left(\frac{1-H}{H}\right) + \exp(-L_{t-1}) - \log\left(\frac{1-H}{H}\right) - \exp(L_{t-1}) \quad (2)$$

<sup>369</sup> The  $LLR$  was computed from inputs  $s_t$  by applying a sigmoid function defined by parameter

<sup>370</sup>  $\alpha$  that controls the sensitivity of perception to the available sensory information (see Methods  
<sup>371</sup> for details on  $s_t$  in humans and mice):

$$u_t = \frac{1}{1 + \exp(-\alpha * s_t)} \quad (3)$$

$$LLR_t = \log\left(\frac{u_t}{1 - u_t}\right) \quad (4)$$

<sup>372</sup> To allow for bimodal inference, i.e., alternating periods of internally- and externally-biased  
<sup>373</sup> modes of perceptual processing that occur irrespective of the sequence of preceding experiences,  
<sup>374</sup> we assumed that likelihood and prior vary in their influence on the perceptual decision  
<sup>375</sup> according to fluctuations governed by  $\omega_{LLR}$  and  $\omega_\psi$ . These anti-phase sine functions (defined  
<sup>376</sup> by amplitudes  $a_{LLR/\psi}$ , frequency  $f$  and phase  $p$ ) determine the precision afforded to the  
<sup>377</sup> likelihood and prior<sup>53</sup>. The implicit anti-phase fluctuations are mandated by Bayes-optimal  
<sup>378</sup> formulations in which inference depends only on the relative values of prior and likelihood  
<sup>379</sup> precision (i.e., the Kalman gain<sup>54</sup>). As such,  $\omega_{LLR}$  and  $\omega_\psi$  implement a hyperprior<sup>55</sup> in which  
<sup>380</sup> the likelihood and prior precisions are shifted against each other at a dominant timescale  
<sup>381</sup> defined by  $f$ :

$$\omega_{LLR} = a_{LLR} * \sin(f * t + p) + 1 \quad (5)$$

$$\omega_\psi = a_\psi * \sin(f * t + p + \pi) + 1 \quad (6)$$

<sup>382</sup> Finally, a sigmoid transform of the posterior  $L_t$  yields the probability of observing the  
<sup>383</sup> perceptual decision  $y_t$  at a temperature determined by  $\zeta^{-1}$ :

$$P(y_t = 1) = 1 - P(y_t = 0) = \frac{1}{1 + \exp(-\zeta * L_t)} \quad (7)$$

384 We used a maximum likelihood procedure to fit the bimodal inference model (M1, Figure 1F)  
 385 to the behavioral data from the Confidence database<sup>20</sup> and the IBL database<sup>21</sup>, optimizing  
 386 the parameters  $\alpha$ ,  $H$ ,  $amp_{LLR}$ ,  $amp_\psi$ ,  $f$ ,  $p$  and  $\zeta$  (see Methods for details and Supplemental  
 387 Table T2 for a summary of the parameters of the bimodal inference model). We validated  
 388 our model in three steps:

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

395 Model M2 ( $AIC_2 = 9.76 \times 10^4$  in humans and  $4.91 \times 10^4$  in mice) and Model M3 ( $AIC_3 =$   
 396  $1.19 \times 10^5$  in humans and  $5.95 \times 10^4$  in mice) incorporated only oscillations of either likelihood  
 397 or prior precision. Model M4 ( $AIC_4 = 1.69 \times 10^5$  in humans and  $9.12 \times 10^4$  in mice) lacked  
 398 any oscillations of likelihood and prior precision and corresponded to the normative model  
 399 proposed by Glaze et al.<sup>51</sup>. In model M5 ( $AIC_4 = 2.01 \times 10^5$  in humans and  $1.13 \times 10^5$   
 400 in mice), we furthermore removed the integration of information across trials, such that  
 401 perception depended only in incoming sensory information (Figure 1G).

402 The bimodal inference model achieved the lowest AIC across the full model space ( $AIC_1$   
 403  $= 8.16 \times 10^4$  in humans and  $4.24 \times 10^4$  in mice) and was clearly superior to the normative  
 404 Bayesian model of evidence accumulation ( $\delta_{AIC} = -8.79 \times 10^4$  in humans and  $-4.87 \times 10^4$   
 405 in mice; Supplemental Figure S9).

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

model predicted within-training and out-of-training variables. The bimodal inference model characterizes each subject by a sensitivity parameter  $\alpha$  (humans:  $\alpha = 0.5 \pm 1.12 \times 10^{-4}$ ; mice:  $\alpha = 1.06 \pm 2.88 \times 10^{-3}$ ) that captures how strongly perception is driven by the available sensory information, and a hazard rate parameter  $H$  (humans:  $H = 0.45 \pm 4.8 \times 10^{-5}$ ; mice:  $H = 0.46 \pm 2.97 \times 10^{-4}$ ) that controls how heavily perception is biased by perceptual history. The parameter  $f$  captures the dominant time scale at which likelihood (amplitude humans:  $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$ ; mice:  $a_{LLR} = 0.39 \pm 1.08 \times 10^{-3}$ ) and prior precision (amplitude humans:  $a_\psi = 1.44 \pm 5.27 \times 10^{-4}$ ; mice:  $a_\psi = 1.71 \pm 7.15 \times 10^{-3}$ ) fluctuated and was estimated at  $0.11 \pm 1.68 \times 10^{-5} 1/N_{trials}$  and  $0.11 \pm 1.63 \times 10^{-4} 1/N_{trials}$  in mice.

As a sanity check for model fit, we tested whether the frequency of stimulus- and history-congruent trials in the Confidence database<sup>20</sup> and IBL database<sup>21</sup> correlated with the estimated parameters  $\alpha$  and  $H$ , respectively. As expected, the estimated sensitivity toward stimulus information  $\alpha$  was positively correlated with the frequency of stimulus-congruent perceptual choices (humans:  $\beta = 8.4 \pm 0.26$ ,  $T(4.31 \times 10^3) = 32.87$ ,  $p = 1.3 \times 10^{-211}$ ; mice:  $\beta = 1.93 \pm 0.12$ ,  $T(2.07 \times 10^3) = 16.21$ ,  $p = 9.37 \times 10^{-56}$ ). Likewise,  $H$  was negatively correlated with the frequency of history-congruent perceptual choices (humans:  $\beta = -11.84 \pm 0.5$ ,  $T(4.29 \times 10^3) = -23.5$ ,  $p = 5.16 \times 10^{-115}$ ; mice:  $\beta = -6.18 \pm 0.66$ ,  $T(2.08 \times 10^3) = -9.37$ ,  $p = 1.85 \times 10^{-20}$ ).

Our behavioral analyses reveal that humans and mice show significant effects of perceptual history that impaired performance in randomized psychophysical experiments<sup>24,28,30,31,43</sup> (Figure 2A and 3A). We therefore expected that humans and mice underestimated the true hazard rate  $\hat{H}$  of the experimental environments (Confidence database<sup>20</sup>:  $\hat{H}_{Humans} = 0.5 \pm 1.58 \times 10^{-5}$ ); IBL database<sup>21</sup>:  $\hat{H}_{Mice} = 0.49 \pm 6.47 \times 10^{-5}$ ). Indeed, when fitting the bimodal inference model to the trial-wise perceptual choices, we found that the estimated (i.e., subjective) hazard rate  $H$  was lower than  $\hat{H}$  for both humans ( $\beta = -6.87 \pm 0.94$ ,  $T(61.87) = -7.33$ ,  $p = 5.76 \times 10^{-10}$ ) and mice ( $\beta = -2.91 \pm 0.34$ ,  $T(112.57) = -8.51$ ,  $p = 8.65 \times 10^{-14}$ ).

<sup>433</sup> To further probe the validity of the bimodal inference model, we asked whether posterior  
<sup>434</sup> model quantities could explain aspects of the behavioral data that the model was not fitted  
<sup>435</sup> to. We predicted that the posterior decision variable  $L_t$  not only encodes perceptual choices  
<sup>436</sup> (i.e., the variable used for model estimation), but also predicts the speed of response and  
<sup>437</sup> subjective confidence<sup>30,44</sup>. Indeed, the estimated trial-wise posterior decision certainty  $|L_t|$   
<sup>438</sup> correlated negatively with RTs in humans ( $\beta = -4.36 \times 10^{-3} \pm 4.64 \times 10^{-4}$ ,  $T(1.98 \times 10^6)$   
<sup>439</sup>  $= -9.41$ ,  $p = 5.19 \times 10^{-21}$ ) and TDs mice ( $\beta = -35.45 \pm 0.86$ ,  $T(1.28 \times 10^6) = -41.13$ ,  $p$   
<sup>440</sup>  $< 2.2 \times 10^{-308}$ ). Likewise, subjective confidence reports were positively correlated with the  
<sup>441</sup> estimated posterior decision certainty in humans ( $\beta = 7.63 \times 10^{-3} \pm 8.32 \times 10^{-4}$ ,  $T(2.06 \times 10^6)$   
<sup>442</sup>  $= 9.18$ ,  $p = 4.48 \times 10^{-20}$ ).

<sup>443</sup> The dynamic accumulation of information inherent to our model entails that biases toward  
<sup>444</sup> perceptual history are stronger when the posterior decision certainty at the preceding trial is  
<sup>445</sup> high<sup>30,31,51</sup>. Due to the link between posterior decision certainty and confidence, confident  
<sup>446</sup> perceptual choices should be more likely to induce history-congruent perception at the  
<sup>447</sup> subsequent trial<sup>30,31</sup>. In line with our prediction, logistic regression indicated that history-  
<sup>448</sup> congruence was predicted by the posterior decision certainty  $|L_{t-1}|$  extracted from the model  
<sup>449</sup> (humans:  $\beta = 8.22 \times 10^{-3} \pm 1.94 \times 10^{-3}$ ,  $z = 4.25$ ,  $p = 2.17 \times 10^{-5}$ ; mice:  $\beta = -3.72 \times 10^{-3} \pm$   
<sup>450</sup>  $1.83 \times 10^{-3}$ ,  $z = -2.03$ ,  $p = 0.04$ ) and the subjective confidence reported by the participants  
<sup>451</sup> (humans:  $\beta = 0.04 \pm 1.62 \times 10^{-3}$ ,  $z = 27.21$ ,  $p = 4.56 \times 10^{-163}$ ) at the preceding trial.

<sup>452</sup> As a third validation of the bimodal inference model, we used the posterior model parameters  
<sup>453</sup> to simulate synthetic perceptual choices and repeated the behavioral analyses conducted  
<sup>454</sup> for the empirical data. Simulations from the bimodal inference model closely replicated our  
<sup>455</sup> empirical results: Simulated perceptual decisions resulted from a competition of perceptual  
<sup>456</sup> history with incoming sensory signals (Figure 4A). Stimulus- and history-congruence were  
<sup>457</sup> significantly autocorrelated (Figure 4B-C), fluctuating in anti-phase as a scale-invariant  
<sup>458</sup> process with a 1/f power law (Figure 4D-F). Simulated posterior certainty<sup>28,30,44</sup> (i.e., the

<sup>459</sup> absolute of the log posterior ratio  $|L_t|$ ) showed a quadratic relationship to the mode of sensory  
<sup>460</sup> processing (Figure 4H), mirroring the relation of RTs and confidence reports to external and  
<sup>461</sup> internal biases in perception (Figure 2G-H and Figure 3G-H). Crucially, the overlap between  
<sup>462</sup> empirical and simulated data broke down when we removed the anti-phase oscillations or the  
<sup>463</sup> accumulation of evidence over time from the bimodal inference model (Supplemental Figures  
<sup>464</sup> S10-13).

<sup>465</sup> In sum, computational modeling suggested that between-mode fluctuations are best explained  
<sup>466</sup> by two interlinked processes (Figure 1E and F): (i), the dynamic accumulation of information  
<sup>467</sup> across successive trials mandated by normative Bayesian models of evidence accumulation  
<sup>468</sup> and, (ii), ongoing anti-phase oscillations in the impact of external and internal information.

## <sup>469</sup> 6 Discussion

<sup>470</sup> This work investigates the behavioral and computational characteristics of ongoing fluctuations  
<sup>471</sup> in perceptual decision-making using two large-scale datasets in humans<sup>20</sup> and mice<sup>21</sup>. We  
<sup>472</sup> found that humans and mice cycle through recurring intervals of reduced sensitivity to  
<sup>473</sup> external sensory information, during which they rely more strongly on perceptual history, i.e.,  
<sup>474</sup> an internal prediction that is provided by the sequence of preceding choices. Computational  
<sup>475</sup> modeling indicated that these slow periodicities are governed by two interlinked factors: (i),  
<sup>476</sup> the dynamic integration of sensory inputs over time and, (ii), anti-phase oscillations in the  
<sup>477</sup> strength at which perception is driven by internal versus external sources of information.  
<sup>478</sup> These cross-species results suggest that ongoing fluctuations in perceptual decision-making  
<sup>479</sup> arise not merely as a noise-related epiphenomenon of limited processing capacity, but result  
<sup>480</sup> from a structured and adaptive mechanism that fluctuates between internally- and externally-  
<sup>481</sup> 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 choices<sup>22–28,30,32,33</sup>. 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 designs<sup>24,28,30,31,43</sup> (Figures 2A and 3A), we found that perceptual history facilitates post-  
489 perceptual processes such as speed of response<sup>42</sup> (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 performance<sup>6–11</sup>.

498 In computational terms, serial dependencies may leverage the temporal autocorrelation of  
499 natural environments<sup>31,46</sup> to increase the efficiency of decision-making<sup>35,43</sup>. Such temporal  
500 smoothing<sup>46</sup> of sensory inputs may be achieved by updating dynamic predictions about the  
501 world based on the sequence of noisy perceptual experiences<sup>22,31</sup>, using algorithms based on  
502 sequential Bayes<sup>25,42,51</sup> such as Kalman<sup>35</sup> or Hierarchical Gaussian filtering<sup>54</sup>. 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 levels<sup>56</sup>.

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 environment<sup>57</sup>. Akin to the wake-sleep-algorithm  
509 in machine learning<sup>58</sup>, 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 inputs<sup>18</sup>.  
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-cycles<sup>58</sup>. 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 monitoring<sup>59</sup>.

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 accumulation<sup>51</sup> allowed us to quantify the dominant timescale of periodic fluctuations  
535 mode at approximately  $0.11 \sqrt{1/N_{trials}}$  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 point<sup>51</sup> or the drift rate  
546 of evidence accumulation<sup>32</sup>. 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 diffusion<sup>60</sup>, 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 point<sup>60</sup>.

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 continuous<sup>61</sup> or discrete<sup>12</sup> changes in the latent states that modulate perceptual decision-  
564 making at slow timescales. A recent computational study<sup>62</sup> has used a Hidden Markov model  
565 to investigate perceptual decision-making in the IBL database<sup>21</sup>. 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 outcomes<sup>62</sup>. Despite the conceptual  
570 differences to our approach (discrete states in a Hidden Markov model that correspond to  
571 switches between distinct decision-making strategies<sup>62</sup> 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 volatile<sup>19,57</sup>. By  
581 the same token, we suggest that fluctuations in mode occur at the level of perceptual  
582 processing<sup>26,30,46,47</sup>, 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 inference<sup>53</sup>. 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 prior<sup>53</sup>, 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 engagement<sup>63</sup>, which varies according to the availability of cognitive resources that are  
596 modulated by factors such as tonic arousal, familiarity with the task, or fatigue<sup>63</sup>. 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  $0.11 \text{ } 1/N_{trials}$ , which may be compatible with fluctuations in arousal<sup>64</sup>, 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 performance<sup>65</sup>: 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 responses<sup>65</sup>. 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 domains<sup>66–68</sup>, including biases toward perceptual history<sup>28</sup> that we implicate  
612 in internal mode processing. While the increase in response speed and history congruence  
613 over time (Supplemental Section 9.4) 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 size<sup>28,65,66,68–70</sup>, motor behavior<sup>69,70</sup>, or neural data<sup>71</sup>) 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 choices<sup>72</sup>. Such motor-driven priming may lead to errors in randomized  
620 psychophysical designs, resembling the phenomenon that we identify as internally-biased  
621 processing<sup>73</sup>. 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 RTs<sup>72</sup>. 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 confidence<sup>74</sup>. Likewise, perceptual history effects have repeatedly  
627 been replicated in experiments with counter-balanced stimulus-response mappings<sup>30: Feigin2021</sup>.

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 humans<sup>19</sup>,  
639 represent a general phenomenon that occurs across a diverse set of perceptual decision-making  
640 tasks. Our analysis of the Confidence database<sup>20</sup> 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-out<sup>21</sup>. 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 processing<sup>27,75,76</sup>: Short-term attraction may serve the decoding of noisy  
658 sensory inputs and increase the stability of perception, whereas long-term repulsion may

enable efficient encoding and sensitivity to change<sup>27</sup>. In the data analyzed here, history biases tended to be repetitive (Figure 2A, Figure 3A, Supplemental Figure S6 and S7), and only 2 of the 66 experiments of the Confidence database<sup>20</sup> showed significant alternating biases (Supplemental Figure S1). However, as we show in Supplemental Figure S14, fluctuations in both alternating and repeating history biases generate overlapping autocorrelation curves. Our analysis of between-mode fluctuations is therefore not tied exclusively to repeating biases, but accommodates alternating biases as well, such that both may lead to internally-biased processing and reduced sensitivity to external sensory information. Future work could apply our approach to paradigms that boost alternating as opposed to repeating biases, as this would help to better understand how repetition and alternation are linked in terms of their computational function and neural implementation<sup>27</sup>.

A third open question concerns the computational underpinnings of bimodal inference. The addition of slow anti-phase oscillations to the integration of prior and likelihood represents an ad-hoc modification of a normative Bayesian model of evidence accumulation<sup>51</sup>. While the bimodal inference model is supported by formal model comparison, the successful prediction of out-of-training variables and the qualitative reproduction of our empirical data in simulations from posterior model parameters, it is an important task for future research to test (i), whether between-mode fluctuations can emerge spontaneously in hierarchical models of Bayesian inference, (ii), whether modes are continuous<sup>19</sup> or discrete<sup>62</sup>, and (iii), whether bimodal inference can be causally manipulated by experimental variables. We speculate that between-mode fluctuations may separate the perceptual contribution of internal predictions and external sensory data in time, creating unambiguous learning signals that benefit inference about the precision of prior and likelihood, respectively. This proposition should be tested empirically by relating the phenomenon of bimodal inference to performance in, e.g., reversal learning, probabilistic reasoning, or metacognition.

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 problems<sup>18,77</sup> or in calibrating metacognition and reality  
694 monitoring<sup>59</sup>. 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 information<sup>56,78,79</sup> and are typically associated with metacognitive  
697 failures and a departure from consensual reality<sup>79</sup>.

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 (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/>  
707 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 database<sup>20</sup> 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 database<sup>21</sup> 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  $\geq 50\%$ . After exclusion, our  
725 sample consisted of 1.46 million 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  $\pm 5$  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 Database<sup>20</sup>, 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 respond 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 database<sup>21</sup>, we extracted trial durations (TDs) as defined by interval between  
749 stimulus onset and feedback, which represents a coarse measure of RT<sup>21</sup>.

750 **Exclusion criteria for individual data-points:** For non-normalized data (TDs from  
751 the IBL database<sup>21</sup>; d-prime, meta-dprime and M-ratio from the Confidence database<sup>20</sup> and  
752 simulated confidence reports), we excluded data-points that differed from the median by  
753 more than 3 x MAD (median absolute distance<sup>49</sup>). For normalized data (RTs and confidence  
754 reports from the Confidence database<sup>20</sup>), 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 Database<sup>20</sup>, 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 gabor, 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 Database<sup>21</sup>, 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 probabili-  
797 ties 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  $2 * \pi$ ) and squared coherence (frequency-specific  
799 variable that denotes the degree to which the shift between the two time-series is 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  $\pm 5$  trials (i.e., intervals containing a total of 11 trials), we report the  
804 spectral density, coherence and phase for frequencies below  $1/11$   $1/N_{trials}$ . 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  $1/11$   $1/N_{trials}$  (i.e., one value  
808 per subject; data shown in Figure 2E-F and 3E-F).

809 Since the data extracted from the Confidence Database<sup>20</sup> 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  $1/N_{trials}$  rather than cycles per second (Hz). For consistency,  
812 we chose  $1/N_{trials}$  as the unit of frequency for the IBL database<sup>21</sup> as well.

813 **7.4 Quantification and statistical procedures**

814 All aggregate data are reported and displayed with errorbars as mean  $\pm$  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 Database<sup>20</sup>, mixed modeling was conducted using random  
821 intercepts defined for each study. To account for variability across experimental session within  
822 the IBL database<sup>21</sup>, 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 database<sup>20</sup>. By analogy, for the IBL database<sup>21</sup>, we estimated random intercepts  
826 for each session that were nested within the respective mouse. We report  $\beta$  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:

$$y_p = \gamma + (1 - \gamma - \delta) * (\operatorname{erf}(\frac{s_w + \mu}{t}) + 1)/2 \quad (8)$$

837 We used the Broyden–Fletcher–Goldfarb–Shanno algorithm in maximum likelihood  
838 estimation<sup>80</sup> to predict individual choices  $y$  (outcome A:  $y = 0$ ; outcome B:  $y = 1$ ) from the  
839 choice probability  $y_p$ . In humans, we computed  $s_w$  by multiplying the inputs  $s$  (stimulus A:  
840 0; outcome B: 1) with the task difficulty  $D_b$  (binarized across 7 levels):

$$s_w = (s - 0.5) * D_b \quad (9)$$

<sup>841</sup> In mice,  $s_w$  was defined by the respective stimulus contrast in the two hemifields:

$$s_w = Contrast_{Right} - Contrast_{Left} \quad (10)$$

<sup>842</sup> Parameters of the psychometric error function were fitted using the R-package *optimx*<sup>80</sup>. The  
<sup>843</sup> psychometric error function was defined via the parameters  $\gamma$  (lower lapse; lower bound = 0,  
<sup>844</sup> upper bound = 0.5),  $\delta$  (upper lapse; lower bound = 0, upper bound = 0.5),  $\mu$  (bias; lower  
<sup>845</sup> bound humans = -5; upper bound humans = 5, lower bound mice = -0.5, upper bound mice  
<sup>846</sup> = 0.5) and threshold  $t$  (lower bound humans = 0.5, upper bound humans = 25; lower bound  
<sup>847</sup> mice = 0.01, upper bound mice = 1.5).

<sup>848</sup> **7.4.3 Computational modeling**

<sup>849</sup> **Model definition:** Our modeling analysis is an extension of a model proposed by Glaze et  
<sup>850</sup> al.<sup>51</sup>, who defined a normative account of evidence accumulation for decision-making. In this  
<sup>851</sup> model, trial-wise choices are explained by applying Bayes theorem to infer moment-by-moment  
<sup>852</sup> changes in the state of environment from trial-wise noisy observations across trials.

<sup>853</sup> Following Glaze et al.<sup>51</sup>, we applied Bayes rule to compute the posterior evidence for the  
<sup>854</sup> two alternative choices (i.e., the log posterior ratio  $L$ ) from the sensory evidence available at  
<sup>855</sup> time-point  $t$  (i.e., the log likelihood ratio  $LLR$ ) with the prior probability  $\psi$ , weighted by the  
<sup>856</sup> respective precision terms  $\omega_{LLR}$  and  $\omega_\psi$ :

$$L_t = LLR_t * \omega_{LLR} + \psi_t(L_{t-1}, H) * \omega_\psi \quad (11)$$

<sup>857</sup> 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 here<sup>20,21</sup>,  
 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.<sup>51</sup>, the prior  $\psi$  is thus computed as follows:

$$\psi_t(L_{t-1}, H) = L_{t-1} + \log\left(\frac{1-H}{H} + \exp(-L_{t-1})\right) - \log\left(\frac{1-H}{H} + \exp(L_{t-1})\right) \quad (12)$$

864 In this model, humans, mice and simulated agents make perceptual choices based on noisy  
 865 observations  $u$ . These are computed by applying a sensitivity parameter  $\alpha$  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  $\alpha$ :

$$u_t = \frac{1}{1 + \exp(-\alpha * (s_t - 0.5))} \quad (13)$$

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

$$s_t = \text{Contrast}_{Right} - \text{Contrast}_{Left} \quad (14)$$

870 As in humans, we derived the input  $u$  by applying a sigmoid function with a sensitivity  
 871 parameter  $\alpha$  to input  $s$ :

$$u_t = \frac{1}{1 + \exp(-\alpha * s_t)} \quad (15)$$

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

873 follows:

$$LLR_t = \log\left(\frac{u_t}{1 - u_t}\right) \quad (16)$$

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.<sup>51</sup> in that it allowed for systematic  
876 fluctuation in the impact of sensory information (i.e.,  $LLR$ ) and the prior probability  
877 of choices  $\psi$  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  $\omega_{LLR} = a_{LLR} * \sin(f * t + phase) + 1$  and  $\omega_\psi = a_\psi * \sin(f * t + phase + \pi) + 1$ .

880 **Model fitting:** In model fitting, we predicted the trial-wise choices  $y_t$  (option A: 0; option B:  
881 1) from inputs  $s$ . To this end, we minimized the log loss between  $y_t$  and the choice probability  
882  $y_{pt}$  in the unit interval.  $y_{pt}$  was derived from  $L_t$  using a sigmoid function defined by the  
883 inverse decision temperature  $\zeta$ :

$$y_{pt} = \frac{1}{1 + \exp(-\zeta * L_t)} \quad (17)$$

884 This allowed us to infer the free parameters  $H$  (lower bound = 0, upper bound = 1; human  
885 posterior =  $0.45 \pm 4.8 \times 10^{-5}$ ; mouse posterior =  $0.46 \pm 2.97 \times 10^{-4}$ ),  $\alpha$  (lower bound  
886 = 0, upper bound = 5; human posterior =  $0.5 \pm 1.12 \times 10^{-4}$ ; mouse posterior =  $1.06 \pm$   
887  $2.88 \times 10^{-3}$ ),  $a_\psi$  (lower bound = 0, upper bound = 10; human posterior =  $1.44 \pm 5.27 \times 10^{-4}$ ;  
888 mouse posterior =  $1.71 \pm 7.15 \times 10^{-3}$ ),  $amp_{LLR}$  (lower bound = 0, upper bound = 10;  
889 human posterior =  $0.5 \pm 2.02 \times 10^{-4}$ ; mouse posterior =  $0.39 \pm 1.08 \times 10^{-3}$ ), frequency  $f$   
890 (lower bound = 1/40, upper bound = 1/5; human posterior =  $0.11 \pm 1.68 \times 10^{-5}$ ; mouse  
891 posterior =  $0.11 \pm 1.63 \times 10^{-4}$ ),  $p$  (lower bound = 0, upper bound =  $2 * \pi$ ; human posterior  
892 =  $2.72 \pm 4.41 \times 10^{-4}$ ; mouse posterior =  $2.83 \pm 3.95 \times 10^{-3}$ ) and inverse decision temperature  $\zeta$   
893 (lower bound = 1, upper bound = 10; human posterior =  $4.63 \pm 1.95 \times 10^{-4}$ ; mouse posterior

<sup>894</sup> =  $4.82 \pm 3.03 \times 10^{-3}$ ) using maximum likelihood estimation with the Broyden–Fletcher–  
<sup>895</sup> Goldfarb–Shanno algorithm as implemented in the R-function *optimx*<sup>80</sup> (see Supplemental  
<sup>896</sup> Table T2 for a description of our model parameters).

<sup>897</sup> We validated the bimodal inference model in three steps: a formal model comparison to  
<sup>898</sup> reduced models based on AIC (Figure 1F-G; Supplemental Figure S9), the prediction of  
<sup>899</sup> within-training (stimulus- and history-congruence) as well as out-of-training variables (RT  
<sup>900</sup> and confidence), and a qualitative reproduction of the empirical data from model simulations  
<sup>901</sup> based on estimated parameters (Figure 4).

<sup>902</sup> **Model comparison.** We assessed the following model space based on AIC:

<sup>903</sup> • The full *bimodal inference model* (M1; Figure 1F) incorporates the influence of sensory  
<sup>904</sup> information according to the parameter  $\alpha$  (likelihood); the integration of evidence across  
<sup>905</sup> trials according to the parameter  $H$  (prior); anti-phase oscillations in between likelihood  
<sup>906</sup> and prior precision according to  $\omega_{LLR}$  and  $\omega_\psi$  with parameters  $a_{LLR}$  (amplitude likelihood  
<sup>907</sup> fluctuation),  $a_\psi$  (amplitude prior fluctuation),  $f$  (frequency) and  $p$  (phase).

<sup>908</sup> • The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the influence of sen-  
<sup>909</sup> sory information according to parameter  $\alpha$  (likelihood); the integration of evidence across  
<sup>910</sup> trials according to parameter  $H$  (prior); oscillations in likelihood precision according  
<sup>911</sup> to  $\omega_{LLR}$  with parameters  $a_{LLR}$  (amplitude likelihood fluctuation),  $f$  (frequency) and  $p$   
<sup>912</sup> (phase).

<sup>913</sup> • The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory  
<sup>914</sup> information according to parameter  $\alpha$  (likelihood); the integration of evidence across  
<sup>915</sup> trials according to parameter  $H$  (prior); oscillations in the prior precision according  
<sup>916</sup> to  $\omega_\psi$  with parameters  $a_\psi$  (amplitude prior fluctuation),  $f$  (frequency) and  $p$  (phase).

<sup>917</sup> Please note that all models M1-3 lead to shifts in the relative precision of likelihood and  
<sup>918</sup> prior.

- 919 • The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the influence of  
 920 sensory information according to parameter  $\alpha$  (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 scheme<sup>51</sup>.  
 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  $\alpha$  (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.

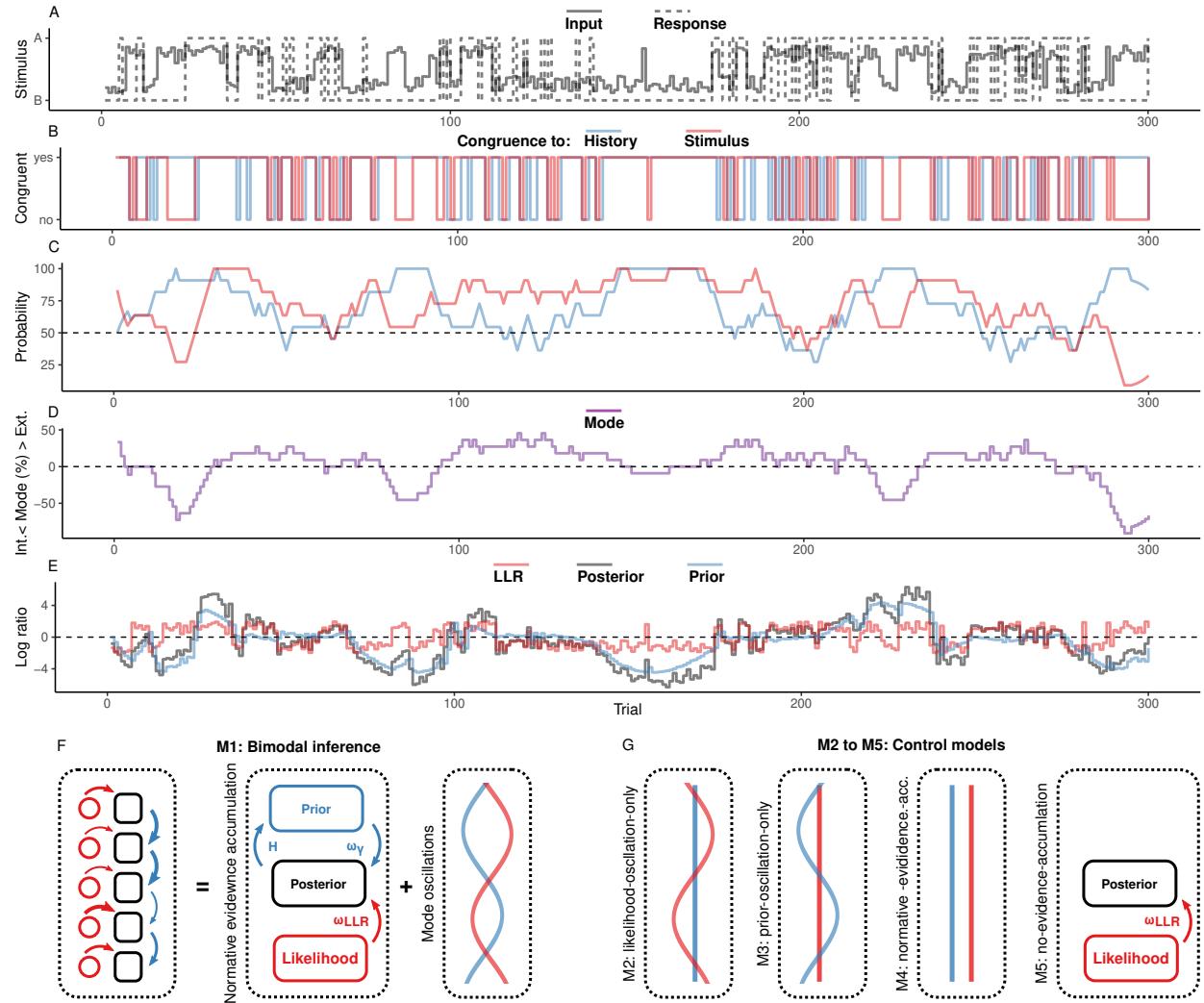
932 **Prediction of within-training and out-of-training variables.** To validate our model, we  
 933 correlated individual posterior parameter estimates with the respective conventional variables.  
 934 As a sanity check, we tested (i), whether the estimated hazard rate  $H$  correlated negatively  
 935 with the frequency of history-congruent choices and, (ii), whether the estimated sensitivity to  
 936 sensory information  $\alpha$  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  $a_\psi$ ,  $a_{LLR}$ ,  
 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 ( $H$ ,  $\alpha$ ,  $a_\psi$ ,  $a_{LLR}$ ,  $f$ ,  $p$  and  $\zeta$ ) 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  $\alpha$  to inputs  $s$ , thus generating stimulus-congruent choices in  $71.36 \pm 2.6 \times 10^{-3}\%$   
952 of trials. Choices were simulated based on the trial-wise choice probabilities  $y_p$  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 **8 Figures**

957 **8.1 Figure 1**



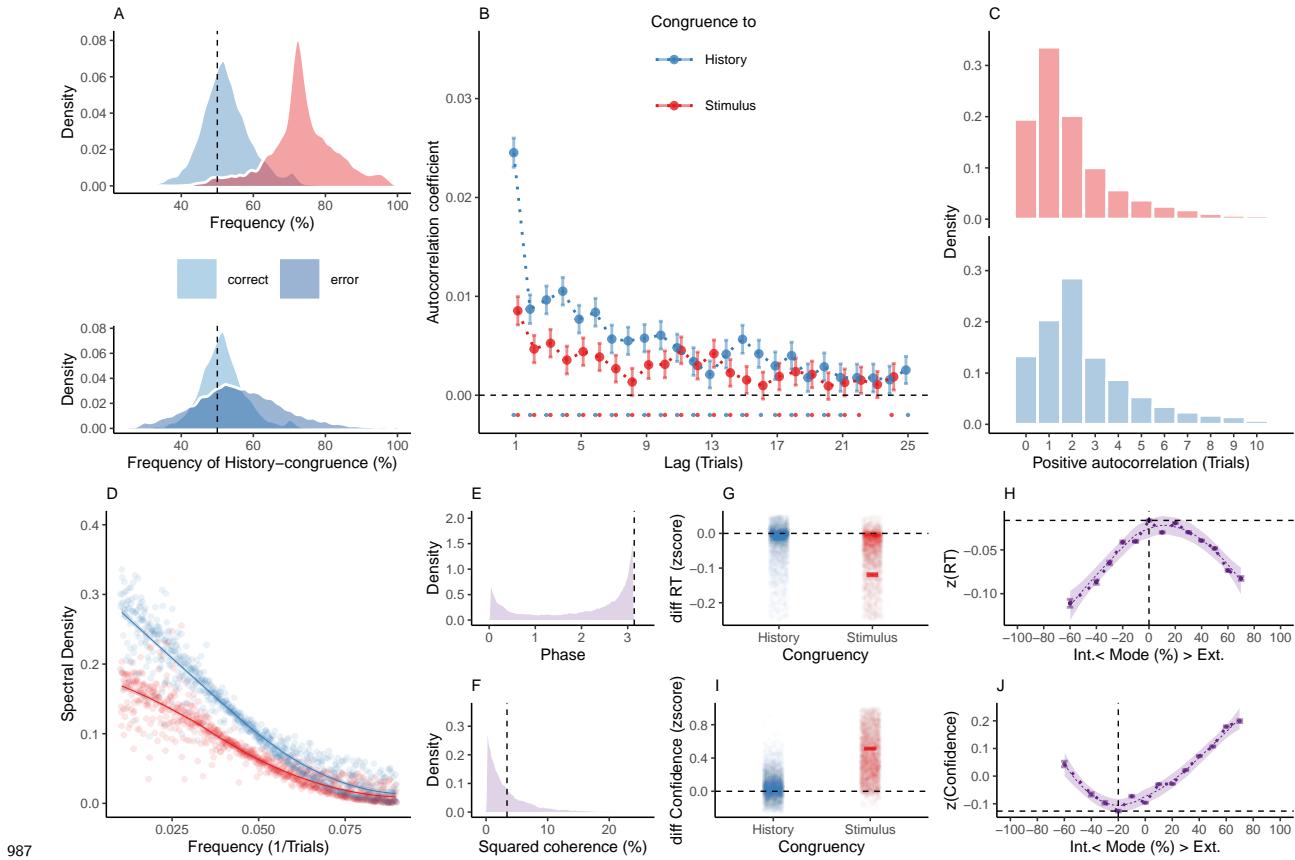
958 **Figure 1. Concept.**

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 (solid 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  $\pm 5$  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  $\omega_{LLR}$  and  $\omega_\psi$  (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.<sup>51</sup>. In the no-evidence-accumulation model (M5), perceptual decisions depend  
985 only on likelihood information (flat priors).

986 **8.2 Figure 2**



987 **Figure 2. Internal and external modes in human perceptual decision-making.**

988 A. In humans, perception was stimulus-congruent in  $73.46\% \pm 0.15\%$  (in red) and history-congruent in  $52.7\% \pm 0.12\%$  of trials (in blue; upper panel). History-congruent perceptual choices were more frequent when perception was stimulus-incongruent (i.e., on *error* trials; lower panel), indicating that history effects impair performance in randomized psychophysical designs.

989 B. Relative to randomly permuted data, we found highly significant autocorrelations of 990 stimulus-congruence and history-congruence (dots indicate intercepts  $\neq 0$  in trial-wise linear 991 mixed effects modeling at  $p < 0.05$ ). Across trials, the autocorrelation coefficients were best 992 fit by an exponential function (adjusted  $R^2$  for stimulus-congruence: 0.53; history-congruence: 993 0.72) as compared to a linear function (adjusted  $R^2$  for stimulus-congruence: 0.53; history- 994 congruence: 0.51), decaying at a rate of  $\gamma = -1.92 \times 10^{-3} \pm 4.5 \times 10^{-4}$  ( $T(6.88 \times 10^4)$ )

<sub>1000</sub>  $= -4.27$ ,  $p = 1.98 \times 10^{-5}$ ) for stimulus-congruence and at a rate of  $\gamma = -6.11 \times 10^{-3} \pm$   
<sub>1001</sub>  $5.69 \times 10^{-4}$  ( $T(6.75 \times 10^4) = -10.74$ ,  $p = 7.18 \times 10^{-27}$ ) for history-congruence.

<sub>1002</sub> C. Here, we depict the number of consecutive trials at which autocorrelation coefficients  
<sub>1003</sub> exceeded the respective autocorrelation of randomly permuted data within individual partici-  
<sub>1004</sub> pants. For stimulus-congruence (upper panel), the lag of positive autocorrelation amounted  
<sub>1005</sub> to  $3.24 \pm 2.39 \times 10^{-3}$  on average, showing a peak at trial  $t+1$  after the index trial. For  
<sub>1006</sub> history-congruence (lower panel), the lag of positive autocorrelation amounted to  $4.87 \pm$   
<sub>1007</sub>  $3.36 \times 10^{-3}$  on average, peaking at trial  $t+2$  after the index trial.

<sub>1008</sub> D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of  $\pm 5$   
<sub>1009</sub> trials) fluctuated as a scale-invariant process with a  $1/f$  power law, i.e., at power densities  
<sub>1010</sub> that were inversely proportional to the frequency.

<sub>1011</sub> E. The distribution of phase shift between fluctuations in stimulus- and history-congruence  
<sub>1012</sub> peaked at half a cycle ( $\pi$  denoted by dotted line).

<sub>1013</sub> F. The average squared coherence between fluctuations in stimulus- and history-congruence  
<sub>1014</sub> (black dotted line) amounted to  $6.49 \pm 2.07 \times 10^{-3}\%$

<sub>1015</sub> G. We observed faster RTs for both stimulus-congruence (as opposed to stimulus-incongruence,  
<sub>1016</sub>  $\beta = -0.14 \pm 1.6 \times 10^{-3}$ ,  $T(1.99 \times 10^6) = -85.84$ ,  $p < 2.2 \times 10^{-308}$ ) and history-congruence  
<sub>1017</sub> ( $\beta = -9.56 \times 10^{-3} \pm 1.37 \times 10^{-3}$ ,  $T(1.98 \times 10^6) = -6.97$ ,  $p = 3.15 \times 10^{-12}$ ).

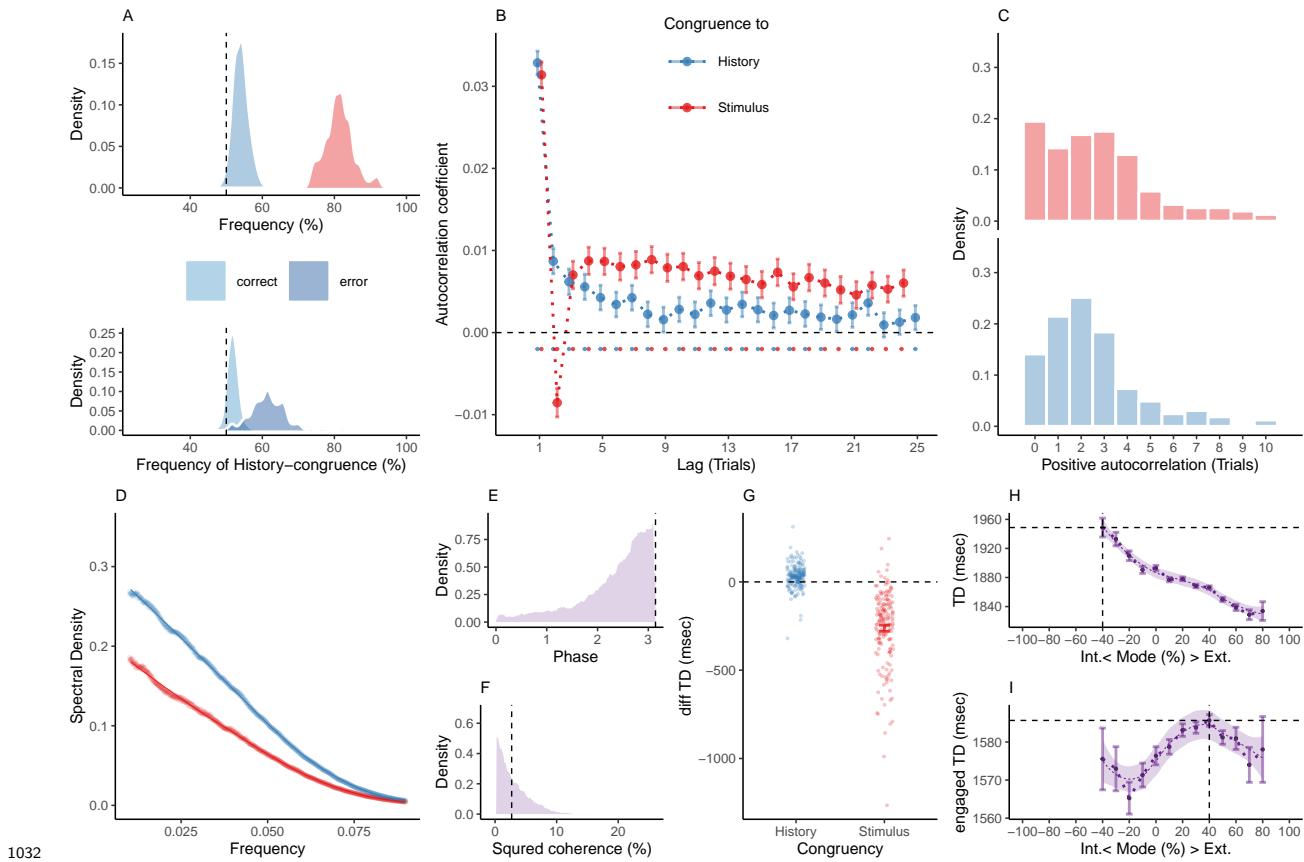
<sub>1018</sub> H. The mode of perceptual processing (i.e., the difference between the smoothed probability  
<sub>1019</sub> of stimulus- vs. history-congruence) showed a quadratic relationship to RTs, with faster  
<sub>1020</sub> RTs for stronger biases toward both external sensory information and internal predictions  
<sub>1021</sub> provided by perceptual history ( $\beta_2 = -19.86 \pm 0.52$ ,  $T(1.98 \times 10^6) = -38.43$ ,  $p = 5 \times 10^{-323}$ ).  
<sub>1022</sub> The horizontal and vertical dotted lines indicate maximum RT and the associated mode,  
<sub>1023</sub> respectively.

<sub>1024</sub> I. Confidence was enhanced for both stimulus-congruence (as opposed to stimulus-

<sub>1025</sub> incongruence,  $\beta = 0.48 \pm 1.38 \times 10^{-3}$ ,  $T(2.06 \times 10^6) = 351.54$ ,  $p < 2.2 \times 10^{-308}$ ) and  
<sub>1026</sub> history-congruence ( $\beta = 0.04 \pm 1.18 \times 10^{-3}$ ,  $T(2.06 \times 10^6) = 36.85$ ,  $p = 3.25 \times 10^{-297}$ ).

<sub>1027</sub> J. In analogy to RTs, we found a quadratic relationship between the mode of perceptual  
<sub>1028</sub> processing and confidence, which increased when both externally- and internally-biased modes  
<sub>1029</sub> grew stronger ( $\beta_2 = 39.3 \pm 0.94$ ,  $T(2.06 \times 10^6) = 41.95$ ,  $p < 2.2 \times 10^{-308}$ ). The horizontal  
<sub>1030</sub> and vertical dotted lines indicate minimum confidence and the associated mode, respectively.

1031 **8.3 Figure 3**



1032 **Figure 3. Internal and external modes in mouse perceptual decision-making.**

1033 A. In mice,  $81.37\% \pm 0.3\%$  of trials were stimulus-congruent (in red) and  $54.03\% \pm 0.17\%$  of trials were history-congruent (in blue; upper panel). History-congruent perceptual choices were not a consequence of the experimental design, but a source of error, as they were more frequent on stimulus-incongruent trials (lower panel).

1034 B. Relative to randomly permuted data, we found highly significant autocorrelations of stimulus-congruence and history-congruence (dots indicate intercepts  $\neq 0$  in trial-wise linear mixed effects modeling at  $p < 0.05$ ). Please note that the negative autocorrelation of stimulus-congruence at trial 2 was a consequence of the experimental design (Supplemental Figure 2D-F). As in humans, autocorrelation coefficients were best fit by an exponential function (adjusted  $R^2$  for stimulus-congruence: 0.44; history-congruence: 0.52) as compared to a linear function (adjusted  $R^2$  for stimulus-congruence:  $3.16 \times 10^{-3}$ ; history-congruence:

1045 0.26), decaying at a rate of  $\gamma = -6.2 \times 10^{-4} \pm 5.93 \times 10^{-4}$  ( $T(3.55 \times 10^4) = -1.05$ ,  $p = 0.3$ )  
1046 for stimulus-congruence and at a rate of  $\gamma = -6.7 \times 10^{-3} \pm 5.94 \times 10^{-4}$  ( $T(3.69 \times 10^4) =$   
1047  $-11.27$ ,  $p = 2.07 \times 10^{-29}$ ) for history-congruence.

1048 C. For stimulus-congruence (upper panel), the lag of positive autocorrelation was longer in  
1049 comparison to humans ( $4.59 \pm 0.06$  on average). For history-congruence (lower panel), the  
1050 lag of positive autocorrelation was slightly shorter relative to humans ( $2.58 \pm 0.01$  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  $\pm 5$  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 ( $\pi$  denoted by dotted line).

1056 F. The average squared coherence between fluctuations in stimulus- and history-congruence  
1057 (black dotted line) amounted to  $3.45 \pm 0.01\%$ .

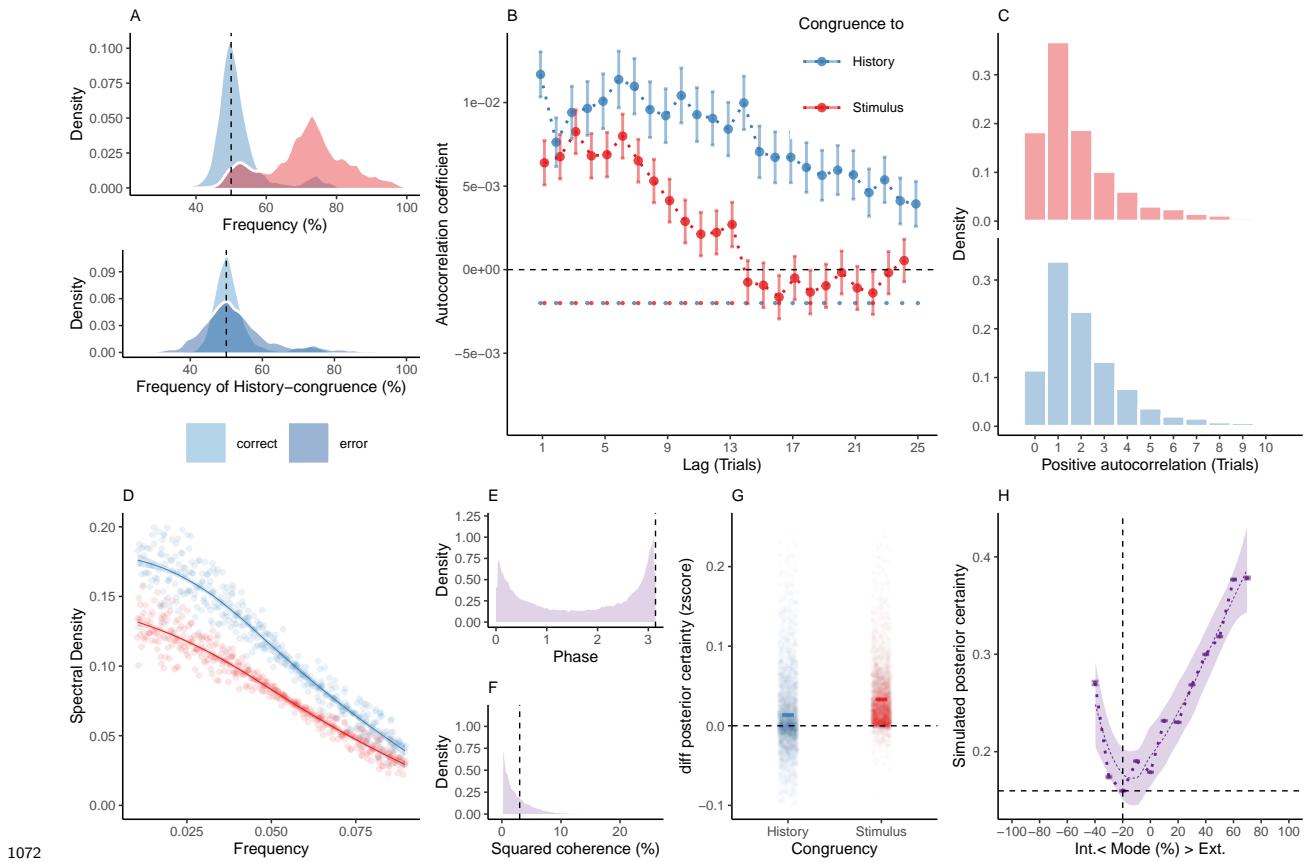
1058 G. We observed shorter trial durations (TDs) for stimulus-congruence (as opposed to stimulus-  
1059 incongruence,  $\beta = -1.12 \pm 8.53 \times 10^{-3}$ ,  $T(1.34 \times 10^6) = -131.78$ ,  $p < 2.2 \times 10^{-308}$ ), but  
1060 longer TDs for history-congruence ( $\beta = 0.06 \pm 6.76 \times 10^{-3}$ ,  $T(1.34 \times 10^6) = 8.52$ ,  $p =$   
1061  $1.58 \times 10^{-17}$ ).

1062 H. TDs decreased monotonically for stronger biases toward external mode ( $\beta_1 = -4.16 \times 10^4$   
1063  $\pm 1.29 \times 10^3$ ,  $T(1.35 \times 10^6) = -32.31$ ,  $p = 6.03 \times 10^{-229}$ ). 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  $1.5 \times \text{MAD}$  (median absolute  
1066 distance<sup>49</sup>), mice exhibited a quadratic component in the relationship between the mode of  
1067 sensory processing and TDs ( $\beta_2 = -1.97 \times 10^3 \pm 843.74$ ,  $T(1.19 \times 10^6) = -2.34$ ,  $p = 0.02$ ).  
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

<sub>1070</sub> the associated mode, respectively.

1071 **8.4 Figure 4**



1072 **Figure 4. Internal and external modes in simulated perceptual decision-making.**

1073 A. Simulated perceptual choices were stimulus-congruent in  $71.36\% \pm 0.17\%$  (in red) and  
 1074 history-congruent in  $51.99\% \pm 0.11\%$  of trials (in blue;  $T(4.32 \times 10^3) = 17.42$ ,  $p = 9.89 \times 10^{-66}$ ;  
 1075 upper panel). Due to the competition between stimulus- and history-congruence, history-  
 1076 congruent perceptual choices were more frequent when perception was stimulus-incongruent  
 1077 (i.e., on *error* trials;  $T(4.32 \times 10^3) = 11.19$ ,  $p = 1.17 \times 10^{-28}$ ; lower panel) and thus impaired  
 1078 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  $2.46 \pm 1.17 \times 10^{-3}$

<sub>1084</sub> trials for stimulus-congruence and  $4.24 \pm 1.85 \times 10^{-3}$  trials for history-congruence.

<sub>1085</sub> D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of  $\pm 5$   
<sub>1086</sub> trials) fluctuated as a scale-invariant process with a  $1/f$  power law, i.e., at power densities  
<sub>1087</sub> that were inversely proportional to the frequency (power  $\sim 1/f^\beta$ ; stimulus-congruence:  $\beta =$   
<sub>1088</sub>  $-0.81 \pm 1.18 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -687.58$ ,  $p < 2.2 \times 10^{-308}$ ; history-congruence:  $\beta =$   
<sub>1089</sub>  $-0.83 \pm 1.27 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -652.11$ ,  $p < 2.2 \times 10^{-308}$ ).

<sub>1090</sub> E. The distribution of phase shift between fluctuations in simulated stimulus- and history-  
<sub>1091</sub> congruence peaked at half a cycle ( $\pi$  denoted by dotted line). The dynamic probabilities of  
<sub>1092</sub> simulated stimulus- and history-congruence were therefore were strongly anti-correlated ( $\beta =$   
<sub>1093</sub>  $-0.03 \pm 8.22 \times 10^{-4}$ ,  $T(2.12 \times 10^6) = -40.52$ ,  $p < 2.2 \times 10^{-308}$ ).

<sub>1094</sub> F. The average squared coherence between fluctuations in simulated stimulus- and history-  
<sub>1095</sub> congruence (black dotted line) amounted to  $6.49 \pm 2.07 \times 10^{-3}\%$ .

<sub>1096</sub> G. Simulated confidence was enhanced for stimulus-congruence ( $\beta = 0.03 \pm 1.71 \times 10^{-4}$ ,  
<sub>1097</sub>  $T(2.03 \times 10^6) = 178.39$ ,  $p < 2.2 \times 10^{-308}$ ) and history-congruence ( $\beta = 0.01 \pm 1.5 \times 10^{-4}$ ,  
<sub>1098</sub>  $T(2.03 \times 10^6) = 74.18$ ,  $p < 2.2 \times 10^{-308}$ ).

<sub>1099</sub> H. In analogy to humans, the simulated data showed a quadratic relationship between the  
<sub>1100</sub> mode of perceptual processing and posterior certainty, which increased for stronger external  
<sub>1101</sub> and internal biases ( $\beta_2 = 31.03 \pm 0.15$ ,  $T(2.04 \times 10^6) = 205.95$ ,  $p < 2.2 \times 10^{-308}$ ). The  
<sub>1102</sub> horizontal and vertical dotted lines indicate minimum posterior certainty and the associated  
<sub>1103</sub> mode, respectively.

1104 **9 Supplemental Items**

1105 **9.1 Internal mode processing is driven by choice history as opposed  
1106 to stimulus history**

1107 The main manuscript reports the effects of perceptual history, which we defined as the impact  
1108 of the choice at the preceding trial on the choice at the current trial (henceforth *choice  
1109 history*). *Stimulus history*, which is defined as the impact of the stimulus presented at the  
1110 preceding trial on the choice at the present trial, represents an alternative approach to this.  
1111 Here, we compare the effects of choice history to the effects of stimulus history.

1112 We observed a significant bias toward stimulus history (humans:  $49.76\% \pm 0.1\%$  of trials,  $\beta$   
1113  $= 1.26 \pm 0.94$ ,  $T(373.62) = 1.34$ ,  $p = 0.18$ ; mice:  $51.11\% \pm 0.08\%$  of trials,  $T(164) = 13.4$ ,  $p  
1114 = 3.86 \times 10^{-28}$ ). The bias toward stimulus history was smaller than the bias toward choice  
1115 history (humans:  $\beta = -3.53 \pm 0.5$ ,  $T(66.53) = -7.01$ ,  $p = 1.48 \times 10^{-9}$ ; mice:  $T(164) =  
1116 -17.21$ ,  $p = 1.43 \times 10^{-38}$ ).

1117 The attraction of choices toward both preceding choices and stimuli is expected, as perception  
1118 was *stimulus-congruent* on approximately 75% of trials, causing choices and stimuli to be  
1119 highly correlated. We therefore compared the effects of choice history and stimulus history  
1120 after *stimulus-incongruent* (i.e., *error*) trials, since those trials lead to opposite predictions  
1121 regarding the perceptual choice at the subsequent trial.

1122 As expected from the findings presented in the main manuscript, perceptual choices were  
1123 attracted toward perceptual choices when the inducing trial was stimulus-incongruent (i.e., a  
1124 positive effect of choice history; humans:  $\beta = 0.19 \pm 1.4 \times 10^{-4}$ ,  $z = 1.36 \times 10^3$ ,  $p < 2.2 \times 10^{-308}$ :  
1125 mice:  $\beta = 0.92 \pm 0.01$ ,  $z = 88.82$ ,  $p < 2.2 \times 10^{-308}$ ). By contrast, perceptual choices tended  
1126 to be repelled away from the stimulus presented at preceding stimulus-incongruent trial  
1127 (i.e., a negative effect of stimulus history; humans:  $\beta = -0.19 \pm 0.01$ ,  $z = -16.47$ ,  $p =  
1128 5.99 \times 10^{-61}$ : mice:  $\beta = -0.92 \pm 0.01$ ,  $z = -88.76$ ,  $p < 2.2 \times 10^{-308}$ ). This repulsion of

1129 choices away from stimuli presented at stimulus-incongruent trials confirmed that choices  
1130 (which are anti-correlated to stimuli at stimulus-incongruent trials) were the primary driver  
1131 of attracting serial effects in perception.

1132 In sum, the above results suggest that, in both humans and mice, serial dependencies were  
1133 better explained by the effects of choice history as opposed to the effects of stimulus history.  
1134 This aligns with a result recently published for the IBL database, where mice were shown to  
1135 follow an *action-kernel* as opposed to a *stimulus-kernel* model when integrating information  
1136 across trials<sup>81</sup>.

1137 **9.2 Fluctuations between internal and external mode modulate  
1138 perceptual performance beyond the effect of general response  
1139 biases**

1140 The hypothesis that perception cycles through opposing internally- and externally-biased  
1141 modes is motivated by the assumption that recurring intervals of stronger perceptual history  
1142 temporally reduce the participants' sensitivity to external information. Importantly, the  
1143 history-dependent biases that characterize internal mode processing must be differentiated  
1144 from general response biases. In binary perceptual decision-making, general response biases  
1145 are defined by a propensity to choose one of the two outcomes more often than the alternative.  
1146 Indeed, human participants selected the more frequent of the two possible outcomes in 58.71%  
1147  $\pm$  0.22% of trials, and mice selected the more frequent of the two possible outcomes in 54.6%  
1148  $\pm$  0.3% of trials.

1149 Two caveats have to be considered to make sure that the effect of history-congruence is  
1150 distinct from the effect of general response biases. First, history-congruent states become  
1151 more likely for larger response biases that cause an increasing imbalance in the likelihood of  
1152 the two outcomes (humans:  $\beta = 0.24 \pm 6.93 \times 10^{-4}$ ,  $T(2.09 \times 10^6) = 342.43$ ,  $p < 2.2 \times 10^{-308}$ ;  
1153 mice:  $\beta = 0.15 \pm 8.25 \times 10^{-4}$ ,  $T(1.32 \times 10^6) = 181.93$ ,  $p < 2.2 \times 10^{-308}$ ). One may thus

ask whether the autocorrelation of history-congruence could be entirely driven by general response biases.

Importantly, our autocorrelation analyses account for general response biases by computing group-level autocorrelations (Figure 2-4B) relative to randomly permuted data (i.e., by subtracting the autocorrelation of randomly permuted data from the raw autocorrelation curve). This precludes that general response biases contribute to the observed autocorrelation of history-congruence (see Supplemental Figure S5 for a visualization of the correction procedure for simulated data with general response biases ranging from 60 to 90%).

Second, it may be argued that fluctuations in perceptual performance may be solely driven by ongoing changes in the strength of general response biases. To assess the links between dynamic fluctuations in stimulus-congruence on the one hand and history-congruence as well as general response bias on the other hand, we computed all variables as dynamic probabilities in sliding windows of  $\pm 5$  trials (Figure 1C). Linear mixed effects modeling indicated that fluctuations in history-congruent biases were larger in amplitude than the corresponding fluctuations in general response biases in humans ( $\beta_0 = 0.03 \pm 7.34 \times 10^{-3}$ ,  $T(64.94) = 4.46$ ,  $p = 3.28 \times 10^{-5}$ ), but slightly smaller in mice ( $\beta_0 = -5.26 \times 10^{-3} \pm 4.67 \times 10^{-4}$ ,  $T(2.12 \times 10^3) = -11.28$ ,  $p = 1.02 \times 10^{-28}$ ).

Crucially, ongoing fluctuations in history-congruence had a significant negative effect on stimulus-congruence (humans:  $\beta_1 = -0.05 \pm 5.63 \times 10^{-4}$ ,  $T(2.1 \times 10^6) = -84.21$ ,  $p < 2.2 \times 10^{-308}$ ; mice:  $\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$ ,  $T(1.34 \times 10^6) = -168.39$ ,  $p < 2.2 \times 10^{-308}$ ) beyond the effect of ongoing changes in general response biases (humans:  $\beta_2 = -0.06 \pm 5.82 \times 10^{-4}$ ,  $T(2.1 \times 10^6) = -103.51$ ,  $p < 2.2 \times 10^{-308}$ ; mice:  $\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$ ,  $T(1.34 \times 10^6) = -48.14$ ,  $p < 2.2 \times 10^{-308}$ ). In sum, the above control analyses confirmed that, in both humans and mice, the observed influence of preceding choices on perceptual decision-making cannot be reduced to general response biases.

1179 **9.3 Internal mode is characterized by lower thresholds as well as**  
1180 **by history-dependent changes in biases and lapses**

1181 Random or stereotypical responses may provide an alternative explanation for the reduced  
1182 sensitivity to external sensory information that we attribute to internal mode processing. To  
1183 test this hypothesis, we asked whether history-independent changes in biases and lapses may  
1184 provide an alternative explanation of the reduced sensitivity during internal mode.

1185 To this end, we estimated full and history-conditioned psychometric curves to investigate how  
1186 internal and external mode relate to biases (i.e., the horizontal position of the psychometric  
1187 curve), lapses (i.e., the asymptotes of the psychometric curve) and thresholds (i.e., 1/sensitivity,  
1188 estimated from the slope of the psychometric curve). We used a maximum likelihood procedure  
1189 to predict trial-wise choices  $y$  ( $y = 0$  and  $y = 1$  for outcomes A and B respectively) from  
1190 the choice probabilities  $y_p$ .  $y_p$  was computed from the difficulty-weighted inputs  $s_w$  via a  
1191 parametric error function defined by the parameters  $\gamma$  (lower lapse),  $\delta$  (upper lapse),  $\mu$  (bias)  
1192 and  $t$  (threshold; see Methods for details):

$$y_p = \gamma + (1 - \gamma - \delta) * (\text{erf}\left(\frac{s_w + \mu}{t}\right) + 1)/2 \quad (18)$$

1193 Under our main hypothesis that periodic reductions in sensitivity to external information  
1194 are driven by increases in the impact of perceptual history, one would expect (i) a history-  
1195 dependent increase in biases and lapses (effects of perceptual history), and (ii), a history-  
1196 independent increase in threshold (reduced sensitivity to external information). Conversely,  
1197 if what we identified as internal mode processing was in fact driven by random choices, one  
1198 would expect (i), a history-independent increase in lapses (choice randomness), (ii), no change  
1199 in bias (no effect of perceptual history), and (iii), reduced thresholds (reduced sensitivity to  
1200 external information).

1201 **9.3.1 Humans**

1202 Across all data provided by the Confidence database<sup>20</sup> (i.e., irrespective of the preceding  
1203 perceptual choice  $y_{t-1}$ ), biases  $\mu$  were distributed around zero ( $-0.05 \pm 0.03$ ;  $\beta_0 = 7.37 \times 10^{-3}$   
1204  $\pm 0.09$ ,  $T(36.8) = 0.08$ ,  $p = 0.94$ ; Supplemental Figure 6A-B, upper panel). When conditioned  
1205 on perceptual history, biases  $\mu$  varied according to the preceding perceptual choice, with  
1206 negative biases for  $y_{t-1} = 0$  ( $-0.22 \pm 0.04$ ;  $\beta_0 = 0.56 \pm 0.12$ ,  $T(43.39) = 4.6$ ,  $p = 3.64 \times 10^{-5}$ ;  
1207 Supplemental Figure 6A-B, upper panel) and positive biases for  $y_{t-1} = 1$  ( $0.29 \pm 0.03$ ;  $\beta_0$   
1208  $= 0.56 \pm 0.12$ ,  $T(43.39) = 4.6$ ,  $p = 3.64 \times 10^{-5}$ ; Supplemental Figure 6A-B, lower panel).  
1209 Absolute biases  $|\mu|$  were larger in internal mode ( $1.84 \pm 0.03$ ) as compared to external  
1210 mode ( $0.86 \pm 0.02$ ;  $\beta_0 = -0.62 \pm 0.07$ ,  $T(45.62) = -8.38$ ,  $p = 8.59 \times 10^{-11}$ ; controlling for  
1211 differences in lapses and thresholds).

1212 Lower and upper lapses amounted to  $\gamma = 0.13 \pm 2.83 \times 10^{-3}$  and  $\delta = 0.1 \pm 2.45 \times 10^{-3}$   
1213 (Supplemental Figure 6A, C and D). Lapses were larger in internal mode ( $\gamma = 0.17 \pm$   
1214  $3.52 \times 10^{-3}$ ,  $\delta = 0.14 \pm 3.18 \times 10^{-3}$ ) as compared to external mode ( $\gamma = 0.1 \pm 2.2 \times 10^{-3}$ ,  $\delta =$   
1215  $0.08 \pm 2 \times 10^{-3}$ ;  $\beta_0 = -0.05 \pm 5.73 \times 10^{-3}$ ,  $T(47.03) = -9.11$ ,  $p = 5.94 \times 10^{-12}$ ; controlling  
1216 for differences in biases and thresholds).

1217 Conditioning on the previous perceptual choice revealed that the between-mode difference in  
1218 lapse was not general, but depended on perceptual history: For  $y_{t-1} = 0$ , only higher lapses  $\delta$   
1219 differed between internal and external mode ( $\beta_0 = -0.1 \pm 9.58 \times 10^{-3}$ ,  $T(36.87) = -10.16$ ,  $p$   
1220  $= 3.06 \times 10^{-12}$ ), whereas lower lapses  $\gamma$  did not ( $\beta_0 = 0.01 \pm 7.77 \times 10^{-3}$ ,  $T(33.1) = 1.61$ ,  $p$   
1221  $= 0.12$ ). Vice versa, for  $y_{t-1} = 1$ , lower lapses  $\gamma$  differed between internal and external mode  
1222 ( $\beta_0 = -0.11 \pm 0.01$ ,  $T(40.11) = -9.59$ ,  $p = 6.14 \times 10^{-12}$ ), whereas higher lapses  $\delta$  did not  
1223 ( $\beta_0 = 0.01 \pm 7.74 \times 10^{-3}$ ,  $T(33.66) = 1.58$ ,  $p = 0.12$ ).

1224 Thresholds  $t$  were estimated at  $3 \pm 0.06$  (Supplemental Figure 6A and E). Thresholds  $t$  were  
1225 larger in internal mode ( $3.66 \pm 0.09$ ) as compared to external mode ( $2.02 \pm 0.03$ ;  $\beta_0 = -1.77$   
1226  $\pm 0.25$ ,  $T(50.45) = -7.14$ ,  $p = 3.48 \times 10^{-9}$ ; controlling for differences in biases and lapses).

<sub>1227</sub> In contrast to the bias  $\mu$  and the lapse rates  $\gamma$  and  $\delta$ , thresholds  $t$  were not modulated by  
<sub>1228</sub> perceptual history ( $\beta_0 = 0.04 \pm 0.06$ ,  $T(2.97 \times 10^3) = 0.73$ ,  $p = 0.47$ ).

<sub>1229</sub> **9.3.2 Mice**

<sub>1230</sub> When estimated based on the full dataset provided in the IBL database<sup>21</sup> (i.e., irrespective  
<sub>1231</sub> of the preceding perceptual choice  $y_{t-1}$ ), biases  $\mu$  were distributed around zero ( $3.87 \times 10^{-3}$   
<sub>1232</sub>  $\pm 9.81 \times 10^{-3}$ ;  $T(164) = 0.39$ ,  $p = 0.69$ ; Supplemental Figure 7A-B, upper panel). When  
<sub>1233</sub> conditioned on the preceding perceptual choice, biases were negative for  $y_{t-1} = 0$  ( $-0.02$   
<sub>1234</sub>  $\pm 8.7 \times 10^{-3}$ ;  $T(164) = -1.99$ ,  $p = 0.05$ ; Supplemental Figure 7A-B, middle panel) and  
<sub>1235</sub> positive for  $y_{t-1} = 1$  ( $0.02 \pm 9.63 \times 10^{-3}$ ;  $T(164) = 1.91$ ,  $p = 0.06$ ; Supplemental Figure  
<sub>1236</sub> 7A-B, lower panel). As in humans, mice showed larger biases during internal mode ( $0.14$   
<sub>1237</sub>  $\pm 7.96 \times 10^{-3}$ ) as compared to external mode ( $0.07 \pm 8.7 \times 10^{-3}$ ;  $\beta_0 = -0.18 \pm 0.03$ ,  $T =$   
<sub>1238</sub>  $-6.38$ ,  $p = 1.77 \times 10^{-9}$ ; controlling for differences in lapses and thresholds).

<sub>1239</sub> Lower and upper lapses amounted to  $\gamma = 0.1 \pm 4.35 \times 10^{-3}$  and  $\delta = 0.11 \pm 4.65 \times 10^{-3}$   
<sub>1240</sub> (Supplemental Figure 7A, C and D). Lapse rates were higher in internal mode ( $\gamma = 0.15 \pm$   
<sub>1241</sub>  $5.14 \times 10^{-3}$ ,  $\delta = 0.16 \pm 5.79 \times 10^{-3}$ ) as compared to external mode ( $\gamma = 0.06 \pm 3.11 \times 10^{-3}$ ,  
<sub>1242</sub>  $\delta = 0.07 \pm 3.34 \times 10^{-3}$ ;  $\beta_0 = -0.11 \pm 4.39 \times 10^{-3}$ ,  $T = -24.8$ ,  $p = 4.91 \times 10^{-57}$ ; controlling  
<sub>1243</sub> for differences in biases and thresholds).

<sub>1244</sub> For  $y_{t-1} = 0$ , the difference between internal and external mode was more pronounced for  
<sub>1245</sub> higher lapses  $\delta$  ( $T(164) = 21.44$ ,  $p = 1.93 \times 10^{-49}$ ). Conversely, for  $y_{t-1} = 1$ , the difference  
<sub>1246</sub> between internal and external mode was more pronounced for lower lapses  $\gamma$  ( $T(164) =$   
<sub>1247</sub>  $-18.24$ ,  $p = 2.68 \times 10^{-41}$ ). In contrast to the human data, higher lapses  $\delta$  and lower lapses  
<sub>1248</sub>  $\gamma$  were significantly elevated during internal mode irrespective of the preceding perceptual  
<sub>1249</sub> choice (higher lapses  $\delta$  for  $y_{t-1} = 1$ :  $T(164) = -2.65$ ,  $p = 8.91 \times 10^{-3}$ ; higher lapses  $\delta$  for  
<sub>1250</sub>  $y_{t-1} = 0$ :  $T(164) = -28.29$ ,  $p = 5.62 \times 10^{-65}$ ; lower lapses  $\gamma$  for  $y_{t-1} = 1$ :  $T(164) = -32.44$ ,  $p$   
<sub>1251</sub>  $= 2.92 \times 10^{-73}$ ; lower lapses  $\gamma$  for  $y_{t-1} = 0$ :  $T(164) = -2.5$ ,  $p = 0.01$ ).

1252 In mice, thresholds  $t$  amounted to  $0.15 \pm 6.52 \times 10^{-3}$  (Supplemental Figure 7A and E) and  
1253 were higher in internal mode ( $0.27 \pm 0.01$ ) as compared to external mode ( $0.09 \pm 4.44 \times 10^{-3}$ ;  
1254  $\beta_0 = -0.28 \pm 0.04$ ,  $T = -7.26$ ,  $p = 1.53 \times 10^{-11}$ ; controlling for differences in biases and  
1255 lapses). Thresholds  $t$  were not modulated by perceptual history ( $T(164) = 0.94$ ,  $p = 0.35$ ).  
1256 In sum, the above analyses showed that, in both humans and mice, internal and external  
1257 mode differ with respect to biases, lapses and thresholds. Internally-biased processing was  
1258 characterized by higher thresholds, indicating a reduced sensitivity to sensory information,  
1259 as well as by larger biases and lapses. Importantly, between-mode differences in biases and  
1260 lapses strongly depended on perceptual history. This confirmed that internal mode processing  
1261 cannot be explained solely on the ground of a general (i.e., history-independent) increase in  
1262 lapses or bias indicative of random or stereotypical responses.

## 1263 **9.4 Internal mode processing can not be reduced to insufficient 1264 task familiarity**

1265 It may be assumed that participants tend to repeat preceding choices when they are not yet  
1266 familiar with the experimental task, leading to history-congruent choices that are caused by  
1267 insufficient training. To assess this alternative explanation, we contrasted the correlates of  
1268 bimodal inference with training effects in humans and mice.

### 1269 **9.4.1 Humans**

1270 In the Confidence database<sup>20</sup>, training effects were visible from RTs that were shortened by  
1271 increasing exposure to the task ( $\beta = -7.53 \times 10^{-5} \pm 6.32 \times 10^{-7}$ ,  $T(1.81 \times 10^6) = -119.15$ ,  $p$   
1272  $< 2.2 \times 10^{-308}$ ). Intriguingly, however, history-congruent choices became more frequent with  
1273 increased exposure to the task ( $\beta = 3.6 \times 10^{-5} \pm 2.54 \times 10^{-6}$ ,  $z = 14.19$ ,  $p = 10^{-45}$ ), speaking  
1274 against the proposition that insufficient training induces seriality in response behavior.

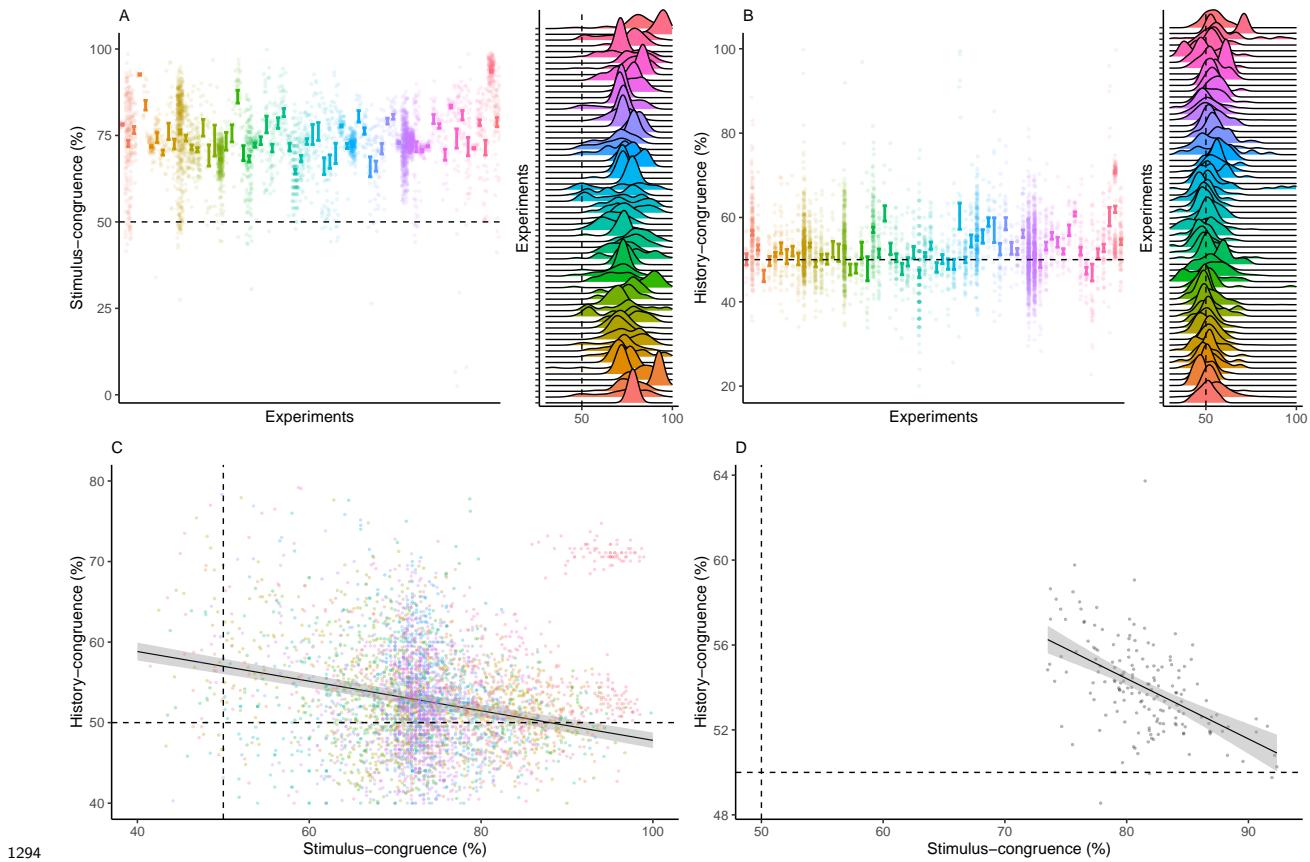
<sub>1275</sub> **9.4.2 Mice**

<sub>1276</sub> As in humans, it is an important caveat to consider whether the observed serial dependencies  
<sub>1277</sub> in mice reflect a phenomenon of perceptual inference, or, alternatively, an unspecific strategy  
<sub>1278</sub> that occurs at the level of reporting behavior. We reasoned that, if mice indeed tended to  
<sub>1279</sub> repeat previous choices as a general response pattern, history effects should decrease during  
<sub>1280</sub> training of the perceptual task. We therefore analyzed how stimulus- and history-congruent  
<sub>1281</sub> perceptual choices evolved across sessions in mice that, by the end of training, achieved  
<sub>1282</sub> proficiency (i.e., stimulus-congruence  $\geq 80\%$ ) in the *basic* task of the IBL dataset<sup>21</sup>.

<sub>1283</sub> Across sessions, we found that stimulus-congruent perceptual choices became more frequent  
<sub>1284</sub> ( $\beta = 0.34 \pm 7.13 \times 10^{-3}$ ,  $T(8.51 \times 10^3) = 47.66$ ,  $p < 2.2 \times 10^{-308}$ ) and TDs were progressively  
<sub>1285</sub> shortened ( $\beta = -22.14 \pm 17.06$ ,  $T(1.14 \times 10^3) = -1.3$ ,  $p < 2.2 \times 10^{-308}$ ). Crucially, the  
<sub>1286</sub> frequency of history-congruent perceptual choices also increased during training ( $\beta = 0.13 \pm$   
<sub>1287</sub>  $4.67 \times 10^{-3}$ ,  $T(8.4 \times 10^3) = 27.04$ ,  $p = 1.96 \times 10^{-154}$ ; Supplemental Figure S8).

<sub>1288</sub> Within individual session, longer task exposure was associated with an increase in history-  
<sub>1289</sub> congruence ( $\beta = 3.6 \times 10^{-5} \pm 2.54 \times 10^{-6}$ ,  $z = 14.19$ ,  $p = 10^{-45}$ ) and a decrease in TDs ( $\beta$   
<sub>1290</sub>  $= -0.1 \pm 3.96 \times 10^{-3}$ ,  $T(1.34 \times 10^6) = -24.99$ ,  $p = 9.45 \times 10^{-138}$ ). In sum, these findings  
<sub>1291</sub> strongly argue against the proposition that mice show biases toward perceptual history due  
<sub>1292</sub> to an unspecific response strategy.

1293 **9.5 Supplemental Figure S1**



1295 **Supplemental Figure S1. Stimulus- and history-congruence.**

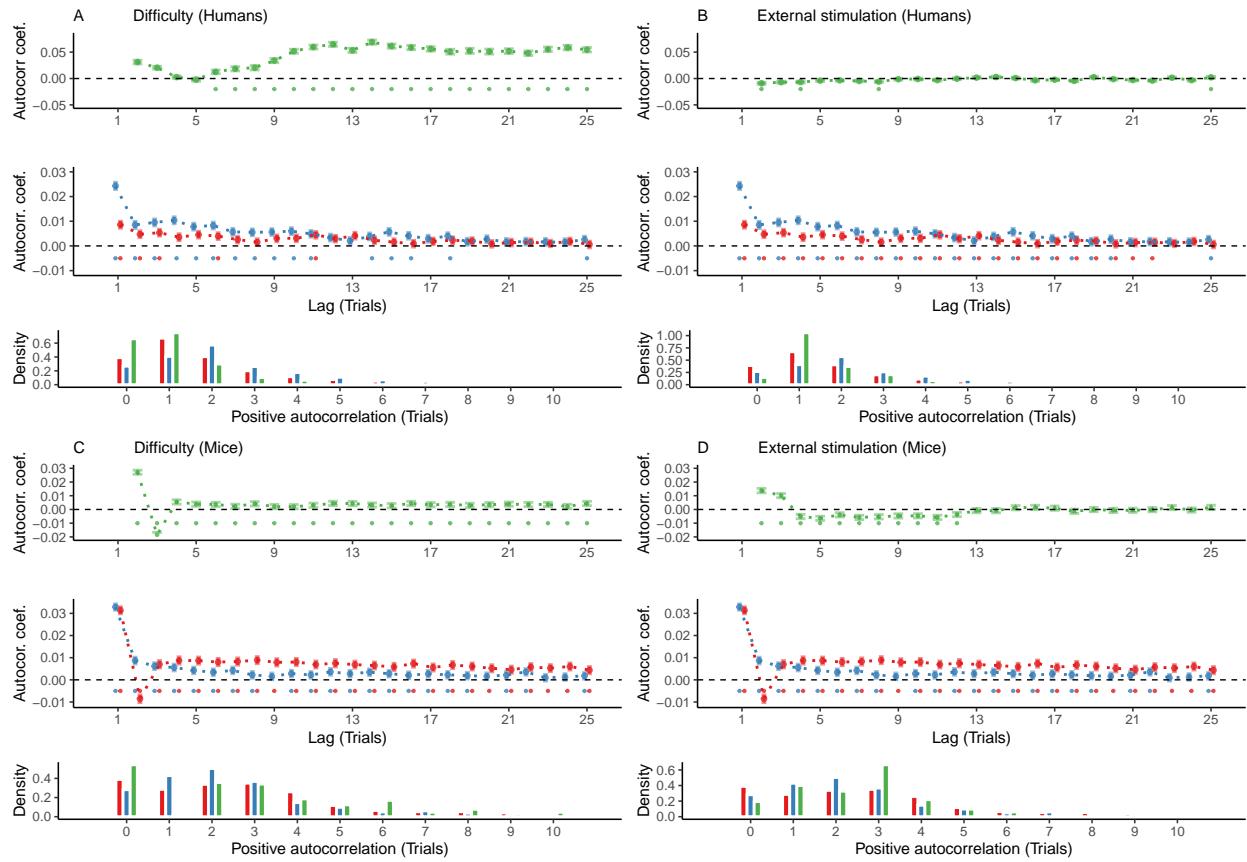
1296 A. Stimulus-congruent choices in humans amounted to  $73.46\% \pm 0.15\%$  of trials and were  
1297 highly consistent across the experiments selected from the Confidence Database.

1298 B. History-congruent choices in humans amounted to  $52.7\% \pm 0.12\%$  of trials. In analogy  
1299 to stimulus-congruence, the prevalence of history-congruence was highly consistent across  
1300 the experiments selected from the Confidence Database. 48.48% of experiments showed  
1301 significant ( $p < 0.05$ ) biases toward preceding choices, whereas 2 of the 66 of the included  
1302 experiments showed significant repelling biases.

1303 C. In humans, we found an enhanced impact of perceptual history in participants who were  
1304 less sensitive to external sensory information ( $T(4.3 \times 10^3) = -14.27$ ,  $p = 3.78 \times 10^{-45}$ ),  
1305 suggesting that perception results from the competition of external with internal information.

<sub>1306</sub> D. In analogy to humans, mice that were less sensitive to external sensory information  
<sub>1307</sub> showed stronger biases toward perceptual history ( $T(163) = -7.52$ ,  $p = 3.44 \times 10^{-12}$ , Pearson  
<sub>1308</sub> correlation).

1309 **9.6 Supplemental Figure S2**



1310 **1311 Supplemental Figure S2. Controlling for task difficulty and external stimulation.**

1312 In this study, we found highly significant autocorrelations of stimulus- and history-congruence  
 1313 in humans as well as in mice, while controlling for task difficulty and the sequence of external  
 1314 stimulation. Here, we confirm that the autocorrelations of stimulus- and history-congruence  
 1315 were not a trivial consequence of the experimental design or the addition of tast difficulty and  
 1316 external stimulation as control variables in the computation of group-level autocorrelations.

1317 A. In humans, task difficulty (in green) showed a significant autocorrelation starting at the  
 1318 5th trial (upper panel, dots at the bottom indicate intercepts  $\neq 0$  in trial-wise linear mixed  
 1319 effects modeling at  $p < 0.05$ ). When controlling for task difficulty only, linear mixed effects  
 1320 modeling indicated a significant autocorrelation of stimulus-congruence (in red) for the first 3  
 1321 consecutive trials (middle panel). 20% of trials within the displayed time window remained  
 1322 significantly autocorrelated. The autocorrelation of history-congruence (in blue) remained

1323 significant for the first 11 consecutive trials (64% significantly autocorrelated trials within  
1324 the displayed time window). At the level of individual participants, the autocorrelation of  
1325 task difficulty exceeded the respective autocorrelation of randomly permuted within a lag of  
1326  $21.66 \pm 8.37 \times 10^{-3}$  trials (lower panel).

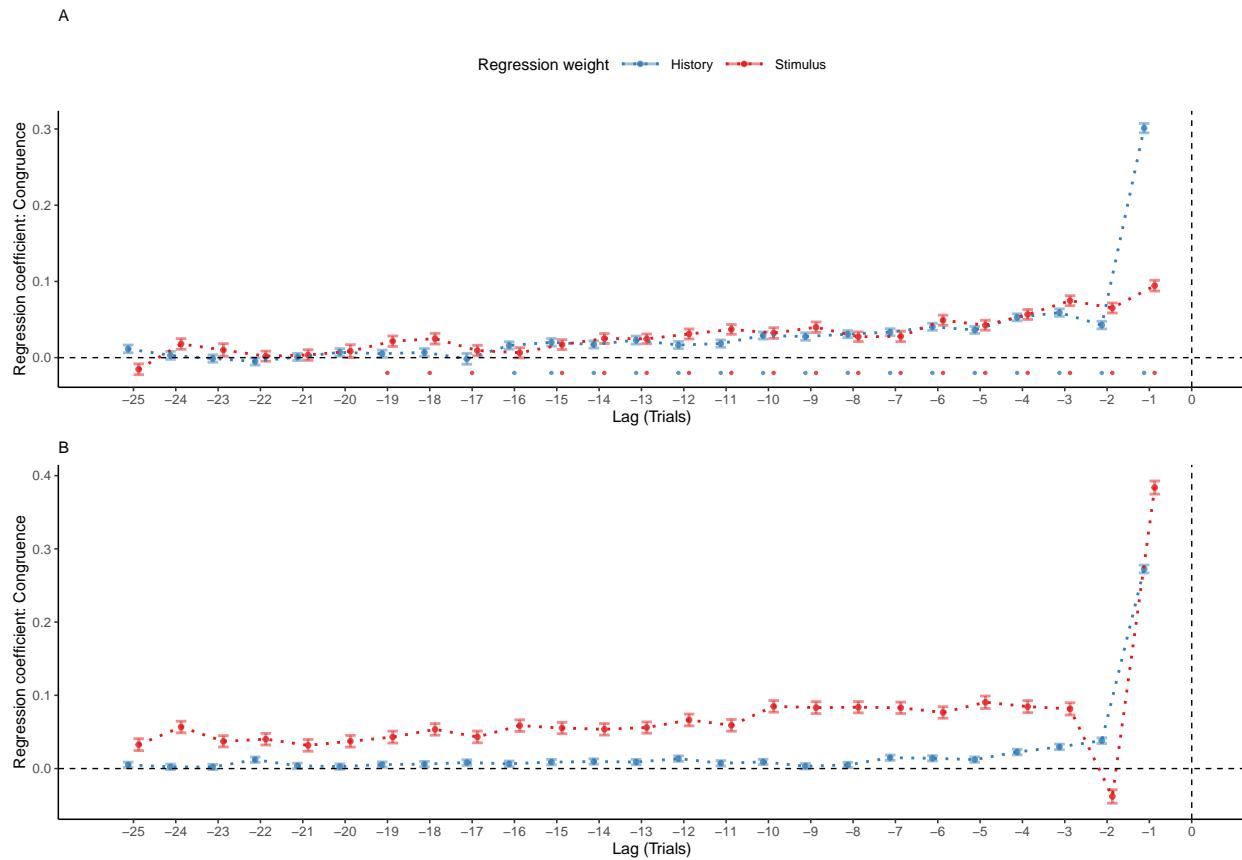
1327 B. In humans, the sequence of external stimulation (i.e., which of the two binary outcomes  
1328 was supported by the presented stimuli; depicted in green) was negatively autocorrelated  
1329 for 1 trial. When controlling for the autocorrelation of external stimulation only, stimulus-  
1330 congruence remained significantly autocorrelated for 22 consecutive trials (88% of trials  
1331 within the displayed time window; lower panel) and history-congruence remained significantly  
1332 autocorrelated for 20 consecutive trials (84% of trials within the displayed time window). At  
1333 the level of individual participants, the autocorrelation of external stimulation exceeded the  
1334 respective autocorrelation of randomly permuted within a lag of  $2.94 \pm 4.4 \times 10^{-3}$  consecutive  
1335 trials (lower panel).

1336 C. In mice, task difficulty showed a significant autocorrelated for the first 25 consecutive trials  
1337 (upper panel). When controlling only for task difficulty only, linear mixed effects modeling  
1338 indicated a significant autocorrelation of stimulus-congruence for the first 36 consecutive trials  
1339 (middle panel). In total, 100% of trials within the displayed time window remained significantly  
1340 autocorrelated. The autocorrelation of history-congruence remained significant for the first  
1341 8 consecutive trials, with 84% significantly autocorrelated trials within the displayed time  
1342 window. At the level of individual mice, autocorrelation coefficients for difficulty were elevated  
1343 above randomly permuted data within a lag of  $15.13 \pm 0.19$  consecutive trials (lower panel).

1344 D. In mice, the sequence of external stimulation (i.e., which of the two binary outcomes was  
1345 supported by the presented stimuli) was negatively autocorrelated for 11 consecutive trials  
1346 (upper panel). When controlling only for the autocorrelation of external stimulation, stimulus-  
1347 congruence remained significantly autocorrelated for 86 consecutive trials (100% of trials  
1348 within the displayed time window; middle) and history-congruence remained significantly

<sub>1349</sub> autocorrelated for 8 consecutive trials (84% of trials within the displayed time window). At  
<sub>1350</sub> the level of individual mice, autocorrelation coefficients for external stimulation were elevated  
<sub>1351</sub> above randomly permuted data within a lag of  $2.53 \pm 9.8 \times 10^{-3}$  consecutive trials (lower  
<sub>1352</sub> panel).

1353 **9.7 Supplemental Figure S3**



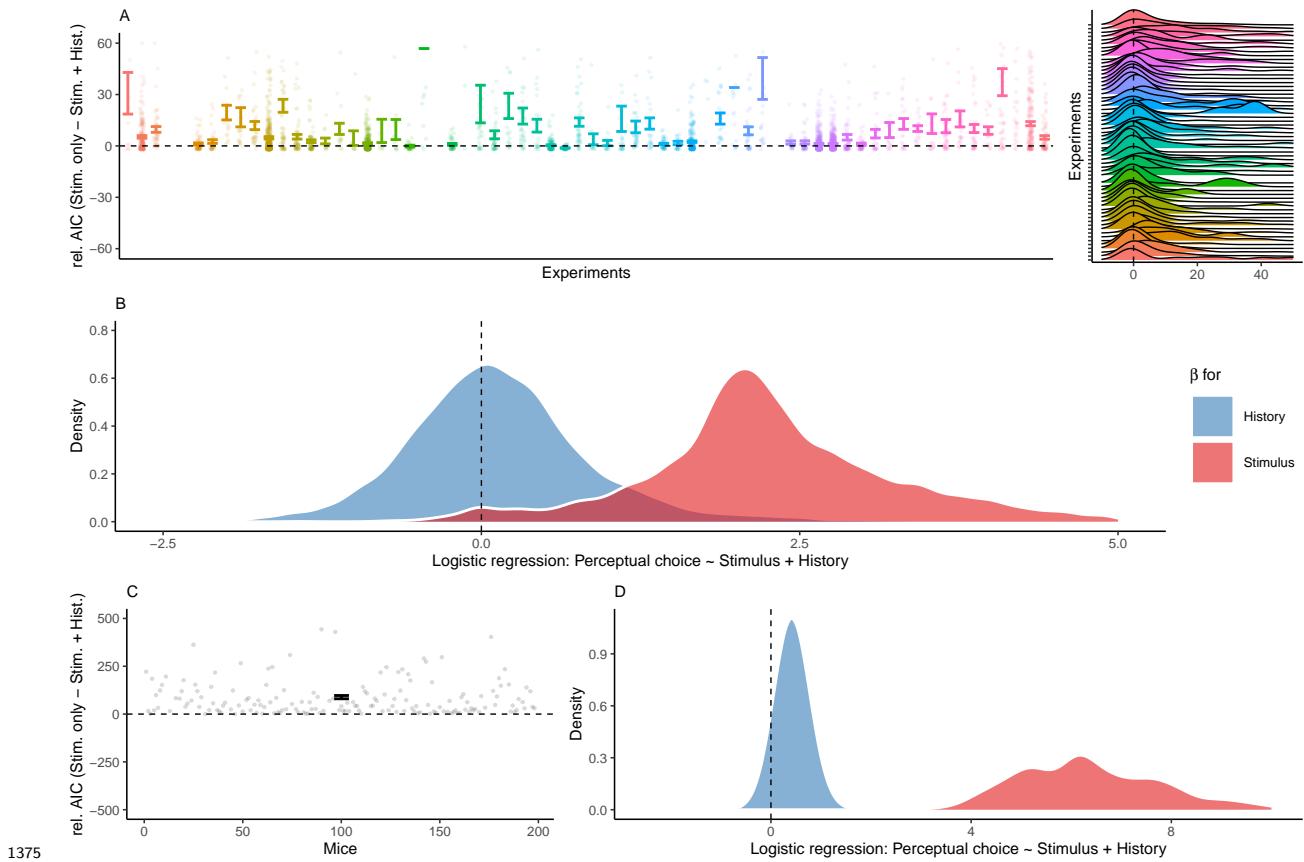
1355 **Supplemental Figure S3. Reproducing group-level autocorrelations using logistic  
1356 regression.**

1357 A. As an alternative to group-level autocorrelation coefficients, we used trial-wise logistic  
1358 regression to quantify serial dependencies in stimulus- and history-congruence. This analysis  
1359 predicted stimulus- and history-congruence at the index trial (trial  $t = 0$ , vertical line) based  
1360 on stimulus- and history-congruence at the 100 preceding trials. Mirroring the shape of the  
1361 group-level autocorrelations, trial-wise regression coefficients (depicted as mean  $\pm$  SEM, dots  
1362 mark trials with regression weights significantly greater than zero at  $p < 0.05$ ) increased  
1363 toward the index trial  $t = 0$  for the human data.

1364 B. Following our results in human data, regression coefficients that predicted history-  
1365 congruence at the index trial (trial  $t = 0$ , vertical line) increased exponentially for trials  
1366 closer to the index trial in mice. In contrast to history-congruence, stimulus-congruence

<sup>1367</sup> showed a negative regression weight (or autocorrelation coefficient; Figure 3B) at trial -2.  
<sup>1368</sup> This was due to the experimental design (see also the autocorrelations of difficulty and  
<sup>1369</sup> external stimulation in Supplemental Figure S2C and D): When mice made errors at easy  
<sup>1370</sup> trials (contrast  $\geq 50\%$ ), the upcoming stimulus was shown at the same spatial location and at  
<sup>1371</sup> high contrast. This increased the probability of stimulus-congruent perceptual choices after  
<sup>1372</sup> stimulus-incongruent perceptual choices at easy trials, thereby creating a negative regression  
<sup>1373</sup> weight (or autocorrelation coefficient) of stimulus-congruence at trial -2.

1374 **9.8 Supplemental Figure S4**



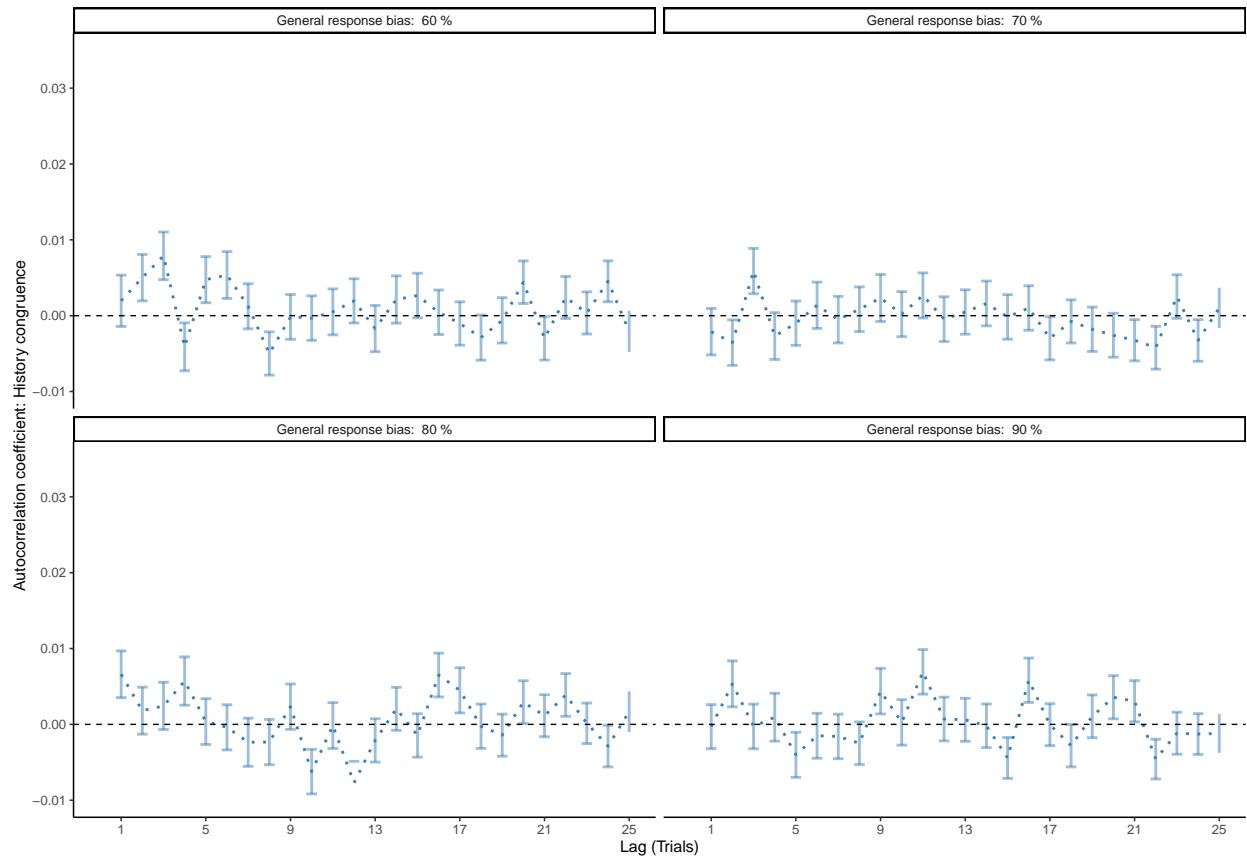
1375 **1376 Supplemental Figure S4. History-congruence in logistic regression.**

1377 A. To ensure that perceptual history played a significant role in perception despite the ongoing  
 1378 stream of external information, we tested whether human perceptual decision-making was  
 1379 better explained by the combination of external and internal information or, alternatively,  
 1380 by external information alone. To this end, we compared AIC between logistic regression  
 1381 models that predicted trial-wise perceptual responses either by both current external sensory  
 1382 information and the preceding percept, or by external sensory information alone (values above  
 1383 zero indicate a superiority of the full model). With high consistency across the experiments  
 1384 selected from the Confidence Database, this model-comparison confirmed that perceptual  
 1385 history contributed significantly to perception (difference in AIC =  $8.07 \pm 0.53$ , T(57.22) =  
 1386 4.1,  $p = 1.31 \times 10^{-4}$ ).

1387 B. Participant-wise regression coefficients amount to  $0.18 \pm 0.02$  for the effect of perceptual

- 1388 history and  $2.51 \pm 0.03$  for external sensory stimulation.
- 1389 C. In mice, an AIC-based model comparison indicated that perception was better explained  
1390 by logistic regression models that predicted trial-wise perceptual responses based on both  
1391 current external sensory information and the preceding percept (difference in AIC =  $88.62 \pm$   
1392  $8.57$ ,  $T(164) = -10.34$ ,  $p = 1.29 \times 10^{-19}$ ).
- 1393 D. In mice, individual regression coefficients amounted to  $0.42 \pm 0.02$  for the effect of  
1394 perceptual history and  $6.91 \pm 0.21$  for external sensory stimulation.

1395 **9.9 Supplemental Figure S5**



1396

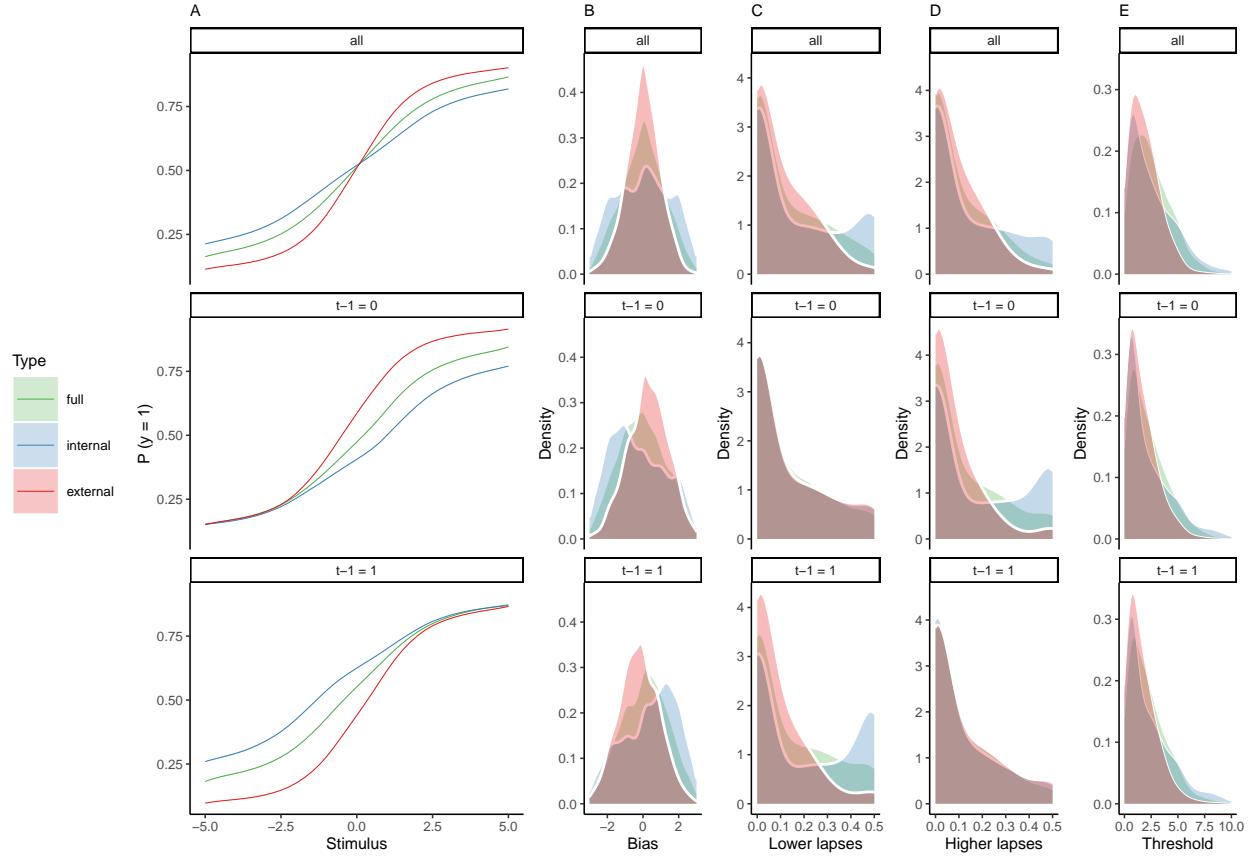
1397 **Supplemental Figure S5. Correcting for general response biases.**

1398 Here, we ask whether the autocorrelation of history-congruence (as shown in Figure 2-3C)  
 1399 may be driven by general response biases (i.e., a general propensity to choose one of the two  
 1400 possible outcomes more frequently than the alternative). To this end, we generated sequences  
 1401 of 100 perceptual choices with general response biases ranging from 60 to 90% for 1000  
 1402 simulated participants each. We then computed the autocorrelation of history-congruence  
 1403 for these simulated data. Crucially, we used the correction procedure that is applied to the  
 1404 autocorrelation curves shown in this manuscript: All reported autocorrelation coefficients are  
 1405 computed relative to the average autocorrelation coefficients obtained for 100 iterations of  
 1406 randomly permuted trial sequences. The above simulation show that this correction procedure  
 1407 removes any potential contribution of general response biases to the autocorrelation of history-  
 1408 congruence. This indicates that the autocorrelation of history-congruence (as shown in Figure

<sub>1409</sub> 2-3C) is not driven by general response biases that were present in the empirical data at a

<sub>1410</sub> level of  $58.71\% \pm 0.22\%$  in humans and  $54.6\% \pm 0.3\%$  in mice.

1411 **9.10 Supplemental Figure S6**



1413 **Supplemental Figure S6. Full and history-conditioned psychometric functions**

1414 **across modes in humans.**

1415 A. Here, we show average psychometric functions for the full dataset (upper panel) and  
 1416 conditioned on perceptual history ( $y_{t-1} = 1$  and  $y_{t-1} = 0$ ; middle and lower panel) across  
 1417 modes (green line) and for internal mode (blue line) and external mode (red line) separately.

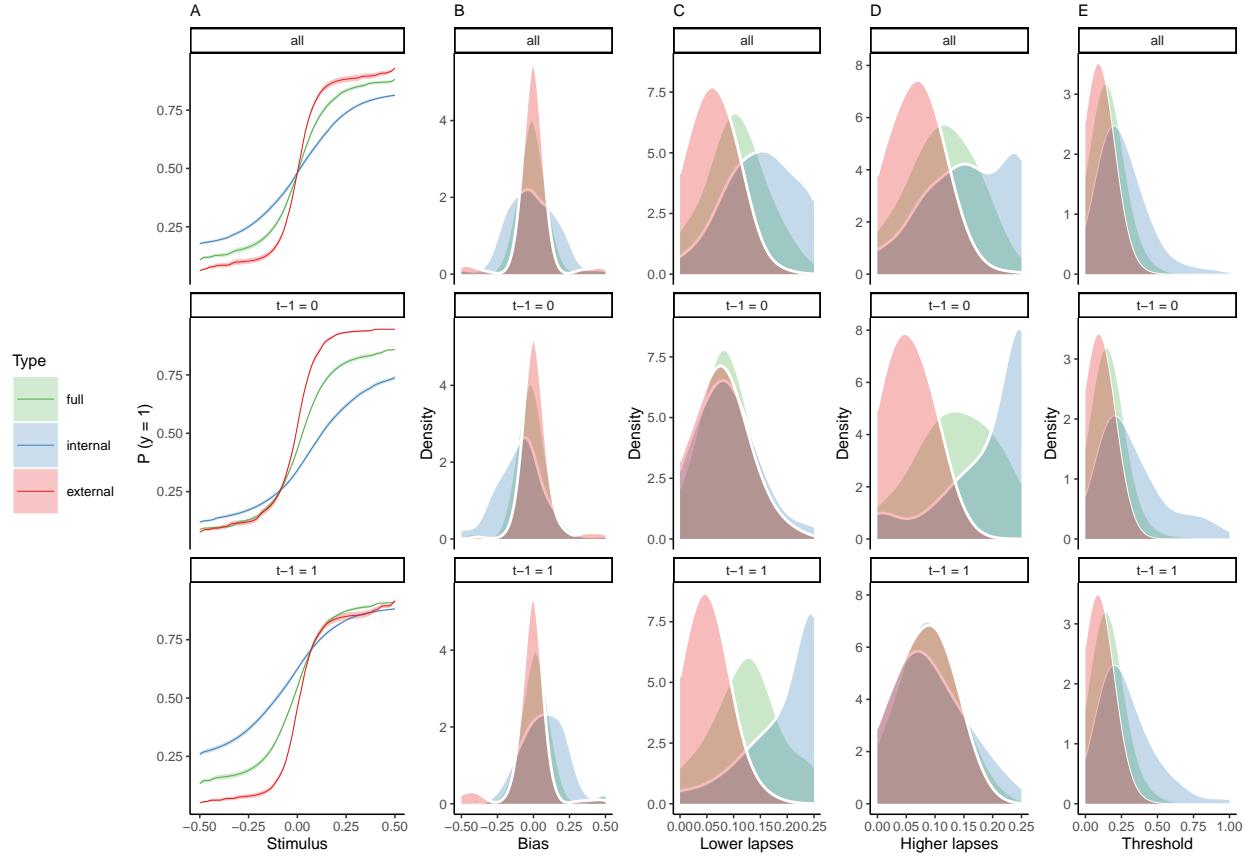
1418 B. Across the full dataset, biases  $\mu$  were distributed around zero ( $\beta_0 = 7.37 \times 10^{-3} \pm 0.09$ ,  
 1419  $T(36.8) = 0.08$ ,  $p = 0.94$ ; upper panel), with larger absolute biases  $|\mu|$  for internal as compared  
 1420 to external mode ( $\beta_0 = -0.62 \pm 0.07$ ,  $T(45.62) = -8.38$ ,  $p = 8.59 \times 10^{-11}$ ; controlling for  
 1421 differences in lapses and thresholds). When conditioned on perceptual history, we observed  
 1422 negative biases for  $y_{t-1} = 0$  ( $\beta_0 = 0.56 \pm 0.12$ ,  $T(43.39) = 4.6$ ,  $p = 3.64 \times 10^{-5}$ ; middle  
 1423 panel) and positive biases for  $y_{t-1} = 1$  ( $\beta_0 = 0.56 \pm 0.12$ ,  $T(43.39) = 4.6$ ,  $p = 3.64 \times 10^{-5}$ ;  
 1424 lower panel).

<sub>1425</sub> C. Lapse rates were higher in internal mode as compared to external mode ( $\beta_0 = -0.05 \pm$   
<sub>1426</sub>  $5.73 \times 10^{-3}$ ,  $T(47.03) = -9.11$ ,  $p = 5.94 \times 10^{-12}$ ; controlling for differences in biases and  
<sub>1427</sub> thresholds; see upper panel and subplot D). Importantly, the between-mode difference in  
<sub>1428</sub> lapses depended on perceptual history: We found no significant difference in lower lapses  
<sub>1429</sub>  $\gamma$  for  $y_{t-1} = 0$  ( $\beta_0 = 0.01 \pm 7.77 \times 10^{-3}$ ,  $T(33.1) = 1.61$ ,  $p = 0.12$ ; middle panel), but a  
<sub>1430</sub> significant difference for  $y_{t-1} = 1$  ( $\beta_0 = -0.11 \pm 0.01$ ,  $T(40.11) = -9.59$ ,  $p = 6.14 \times 10^{-12}$ ;  
<sub>1431</sub> lower panel).

<sub>1432</sub> D. Conversely, higher lapses  $\delta$  were significantly increased for  $y_{t-1} = 0$  ( $\beta_0 = -0.1 \pm$   
<sub>1433</sub>  $9.58 \times 10^{-3}$ ,  $T(36.87) = -10.16$ ,  $p = 3.06 \times 10^{-12}$ ; middle panel), but not for  $y_{t-1} = 1$  ( $\beta_0 =$   
<sub>1434</sub>  $0.01 \pm 7.74 \times 10^{-3}$ ,  $T(33.66) = 1.58$ ,  $p = 0.12$ ; lower panel).

<sub>1435</sub> E. The thresholds  $t$  were larger in internal as compared to external mode ( $\beta_0 = -1.77 \pm 0.25$ ,  
<sub>1436</sub>  $T(50.45) = -7.14$ ,  $p = 3.48 \times 10^{-9}$ ; controlling for differences in biases and lapses) and were  
<sub>1437</sub> not modulated by perceptual history ( $\beta_0 = 0.04 \pm 0.06$ ,  $T(2.97 \times 10^3) = 0.73$ ,  $p = 0.47$ ).

1438 **9.11 Supplemental Figure S7**



1439

1440 **Supplemental Figure S7. Full and history-conditioned psychometric functions**

1441 **across modes in mice.**

1442 A. Here, we show average psychometric functions for the full IBL dataset (upper panel) and  
 1443 conditioned on perceptual history ( $y_{t-1} = 1$  and  $y_{t-1} = 0$ ; middle and lower panel) across  
 1444 modes (green line) and for internal mode (blue line) and external mode (red line) separately.

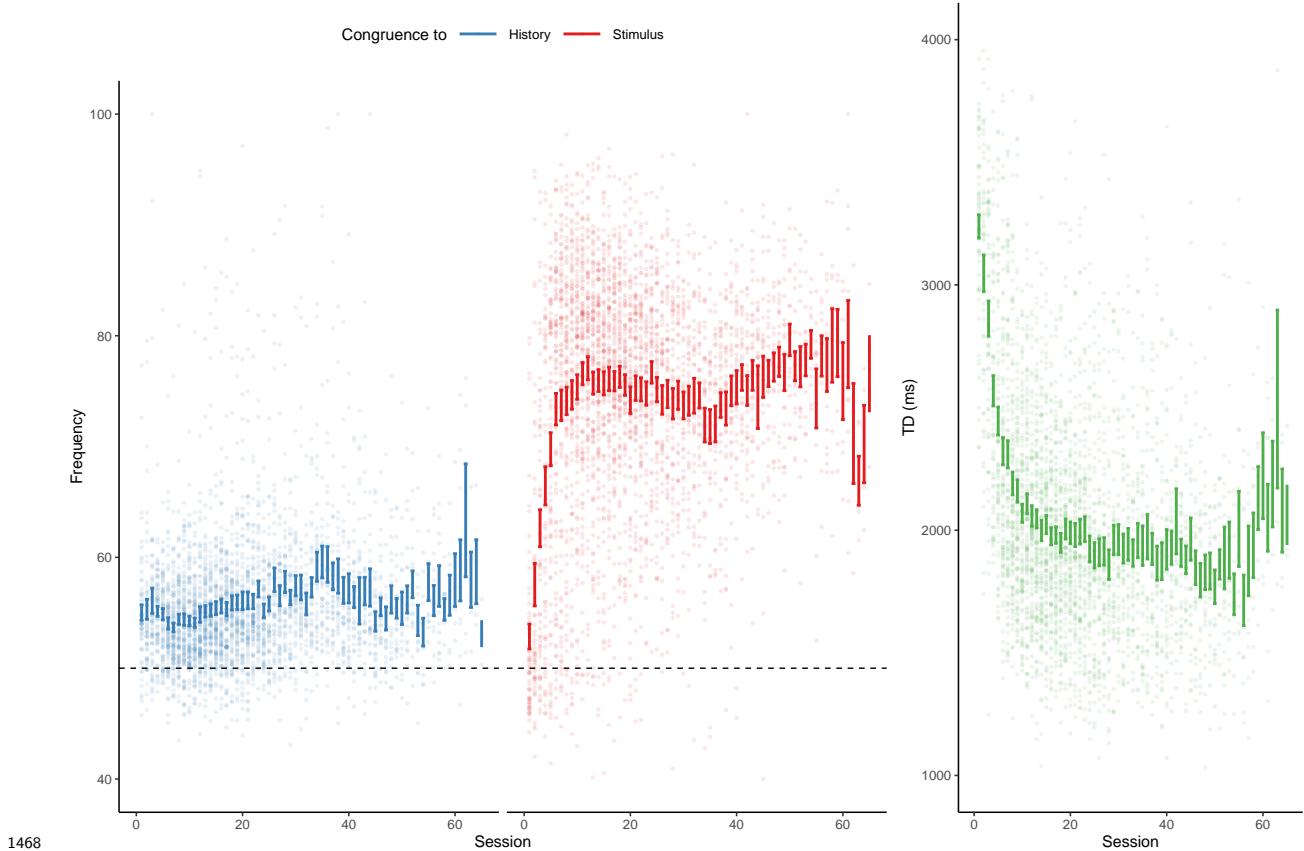
1445 B. Across the full dataset, biases  $\mu$  were distributed around zero ( $T(164) = 0.39$ ,  $p = 0.69$ ;  
 1446 upper panel), with larger absolute biases  $|\mu|$  for internal as compared to external mode ( $\beta_0 =$   
 1447  $-0.18 \pm 0.03$ ,  $T = -6.38$ ,  $p = 1.77 \times 10^{-9}$ ; controlling for differences in lapses and thresholds).  
 1448 When conditioned on perceptual history, we observed negative biases for  $y_{t-1} = 0$  ( $T(164) = 1.91$ ,  $p = 0.05$ ;  
 1449 lower panel) and positive biases for  $y_{t-1} = 1$  ( $T(164) = 1.91$ ,  $p = 0.06$ ;  
 1450 lower panel).

<sub>1451</sub> C. Lapse rates were higher in internal as compared to external mode ( $\beta_0 = -0.11 \pm 4.39 \times 10^{-3}$ ,  
<sub>1452</sub>  $T = -24.8$ ,  $p = 4.91 \times 10^{-57}$ ; controlling for differences in biases and thresholds; upper  
<sub>1453</sub> panel, see subplot D). For  $y_{t-1} = 1$ , the difference between internal and external mode was  
<sub>1454</sub> more pronounced for lower lapses  $\gamma$  ( $T(164) = -18.24$ ,  $p = 2.68 \times 10^{-41}$ ) as compared to  
<sub>1455</sub> higher lapses  $\delta$  (see subplot D). In mice, lower lapses  $\gamma$  were significantly elevated during  
<sub>1456</sub> internal mode irrespective of the preceding perceptual choice (middle panel: lower lapses  $\gamma$   
<sub>1457</sub> for  $y_{t-1} = 0$ ;  $T(164) = -2.5$ ,  $p = 0.01$ , lower panel: lower lapses  $\gamma$  for  $y_{t-1} = 1$ ;  $T(164) =$   
<sub>1458</sub>  $-32.44$ ,  $p = 2.92 \times 10^{-73}$ ).

<sub>1459</sub> D. For  $y_{t-1} = 0$ , the difference between internal and external mode was more pronounced  
<sub>1460</sub> for higher lapses  $\delta$  ( $T(164) = 21.44$ ,  $p = 1.93 \times 10^{-49}$ , see subplot C). Higher lapses were  
<sub>1461</sub> significantly elevated during internal mode irrespective of the preceding perceptual choice  
<sub>1462</sub> (middle panel: higher lapses  $\delta$  for  $y_{t-1} = 0$ ;  $T(164) = -28.29$ ,  $p = 5.62 \times 10^{-65}$  lower panel:  
<sub>1463</sub> higher lapses  $\delta$  for  $y_{t-1} = 1$ ;  $T(164) = -2.65$ ,  $p = 8.91 \times 10^{-3}$ ; ).

<sub>1464</sub> E. Thresholds  $t$  were higher in internal as compared to external mode ( $\beta_0 = -0.28 \pm 0.04$ ,  
<sub>1465</sub>  $T = -7.26$ ,  $p = 1.53 \times 10^{-11}$ ; controlling for differences in biases and lapses) and were not  
<sub>1466</sub> modulated by perceptual history ( $T(164) = 0.94$ ,  $p = 0.35$ ).

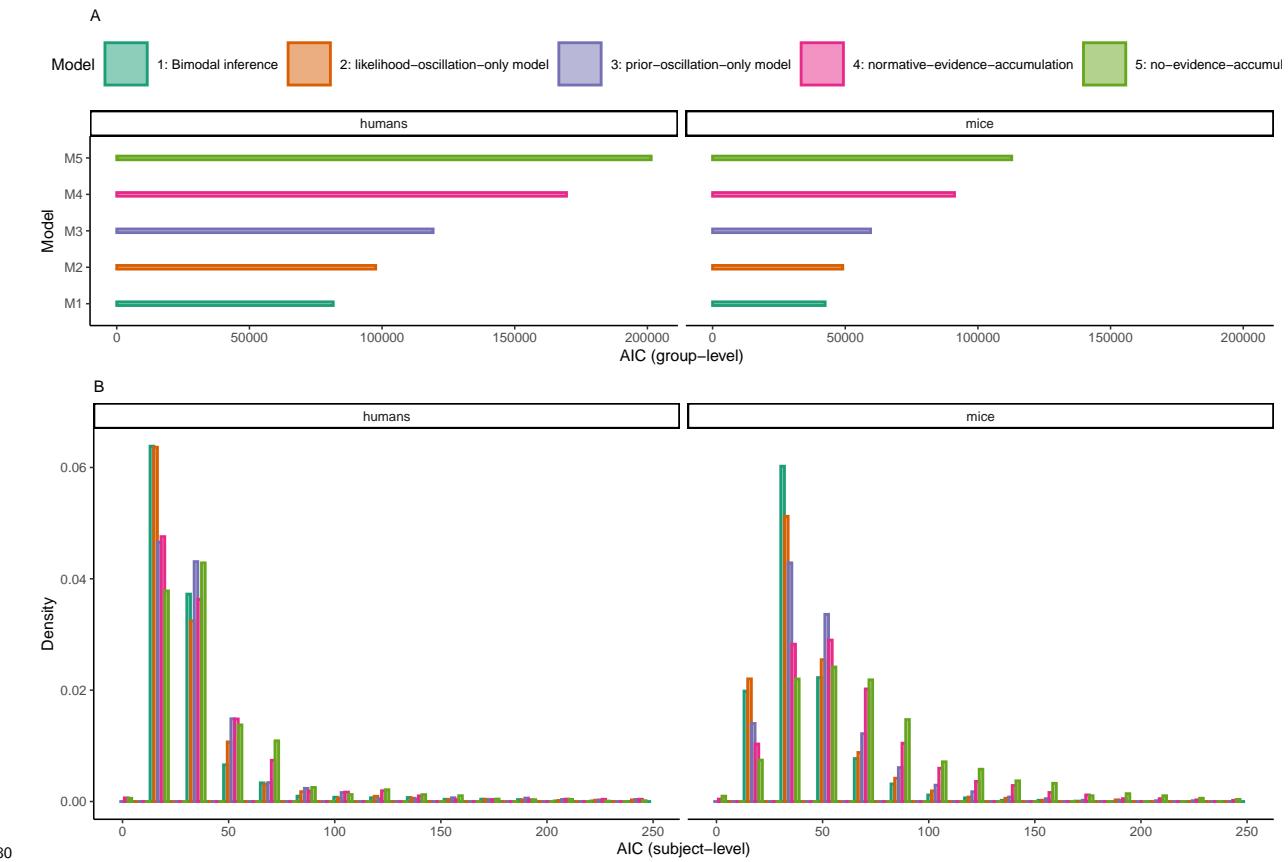
1467 **9.12 Supplemental Figure S8**



1469 **Supplemental Figure S8. History-/stimulus-congruence and TDs during training  
1470 of the basic task.**

1471 Here, we depict the progression of history- and stimulus-congruence (depicted in blue and  
1472 red, respectively; left panel) as well as TDs (in green; right panel) across training sessions in  
1473 mice that achieved proficiency (i.e., stimulus-congruence  $\geq 80\%$ ) in the *basic* task of the IBL  
1474 dataset. We found that both history-congruent perceptual choices ( $\beta = 0.13 \pm 4.67 \times 10^{-3}$ ,  
1475  $T(8.4 \times 10^3) = 27.04$ ,  $p = 1.96 \times 10^{-154}$ ) and stimulus-congruent perceptual choices ( $\beta =$   
1476  $0.34 \pm 7.13 \times 10^{-3}$ ,  $T(8.51 \times 10^3) = 47.66$ ,  $p < 2.2 \times 10^{-308}$ ) became more frequent with  
1477 training. As in humans, mice showed shorter TDs with increased exposure to the task ( $\beta =$   
1478  $-22.14 \pm 17.06$ ,  $T(1.14 \times 10^3) = -1.3$ ,  $p < 2.2 \times 10^{-308}$ ).

1479 **9.13 Supplemental Figure S9**



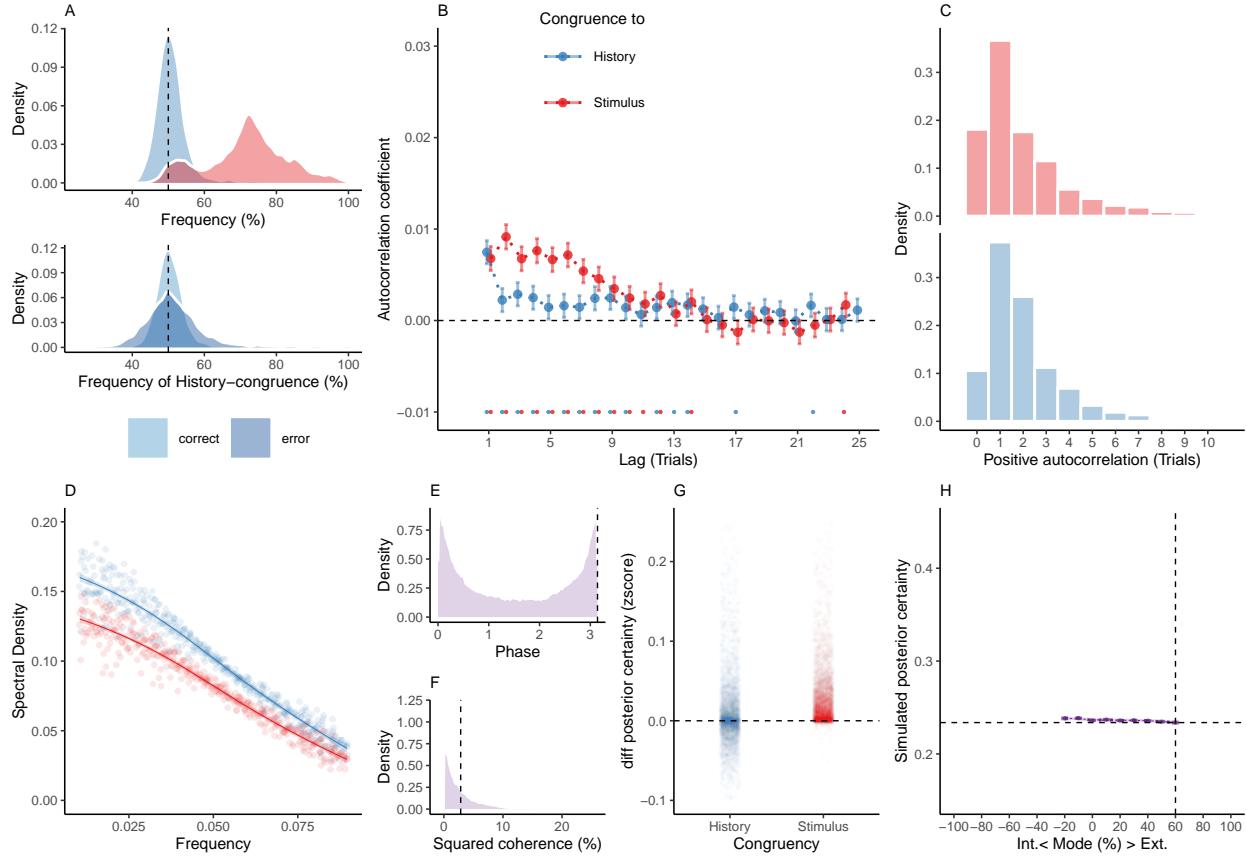
1480 **Supplemental Figure S9. Comparison of the bimodal inference model against reduced control models.**

1481 A. Group-level AIC. The bimodal inference model (M1) achieved the lowest AIC across the  
 1482 full model space ( $AIC_1 = 8.16 \times 10^4$  in humans and  $4.24 \times 10^4$  in mice). Model M2 ( $AIC_2 = 9.76 \times 10^4$  in humans and  $4.91 \times 10^4$  in mice) and Model M3 ( $AIC_3 = 1.19 \times 10^5$  in humans  
 1483 and  $5.95 \times 10^4$  in mice) incorporated only oscillations of either likelihood or prior precision.  
 1484 Model M4 ( $AIC_4 = 1.69 \times 10^5$  in humans and  $9.12 \times 10^4$  in mice) lacked any oscillations of  
 1485 likelihood and prior precision and corresponded to the normative model proposed by Glaze et  
 1486 al.<sup>51</sup>. In model M5 ( $AIC_5 = 2.01 \times 10^5$  in humans and  $1.13 \times 10^5$  in mice), we furthermore  
 1487 removed the integration of information across trials, such that perception depended only in  
 1488 incoming sensory information.

1489 B. Subject-level AIC. Here, we show the distribution of AIC values at the subject-level.

<sub>1493</sub> AIC for the bimodal inference model tended to be smaller than AIC for the comparator  
<sub>1494</sub> models (statistical comparison to the second-best model M2 in humans:  $\beta = -1.71 \pm 0.19$ ,  
<sub>1495</sub>  $T(8.57 \times 10^3) = -8.85$ ,  $p = 1.06 \times 10^{-18}$ ; mice:  $T(1.57 \times 10^3) = -3.08$ ,  $p = 2.12 \times 10^{-3}$ ).

1496 **9.14 Supplemental Figure S10**



1497 **Supplemental Figure S10. Reduced Control Model M2: Only oscillation of the likelihood.** When simulating data for the *likelihood-oscillation-only model*, we removed the oscillation from the prior term by setting the amplitude  $a_\psi$  to zero. Simulated data thus depended only on the participant-wise estimates for hazard rate  $H$ , amplitude  $a_{LLR}$ , frequency  $f$ , phase  $p$  and inverse decision temperature  $\zeta$ .

1503 A. Similar to the full model M1 (Figure 1F and Figure 4), simulated perceptual choices  
 1504 were stimulus-congruent in  $71.97\% \pm 0.17\%$  of trials (in red). History-congruent amounted  
 1505 to  $50.76\% \pm 0.07\%$  of trials (in blue). As in the full model, the likelihood-oscillation-only  
 1506 model showed a significant bias toward perceptual history  $T(4.32 \times 10^3) = 10.29$ ,  $p =$   
 1507  $1.54 \times 10^{-24}$ ; upper panel). Similarly, history-congruent choices were more frequent at error  
 1508 trials ( $T(4.32 \times 10^3) = 9.71$ ,  $p = 4.6 \times 10^{-22}$ ; lower panel).

1509 B. In the likelihood-oscillation-only model, we observed that the autocorrelation coefficients for

1510 history-congruence were reduced below the autocorrelation coefficients of stimulus-congruence.  
1511 This is an approximately five-fold reduction relative to the empirical results observed in humans  
1512 (Figure 2B), where the autocorrelation of history-congruence was above the autocorrelation of  
1513 stimulus-congruence. Moreover, in the reduced model shown here, the number of consecutive  
1514 trials that showed significant autocorrelation of history-congruence was reduced to 11.

1515 C. In the likelihood-oscillation-only model, the number of consecutive trials at which true  
1516 autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted  
1517 data did not differ with respect to stimulus-congruence ( $2.62 \pm 1.39 \times 10^{-3}$  trials;  $T(4.32 \times 10^3)$   
1518 = 1.85,  $p = 0.06$ ), but decreased with respect to history-congruence ( $2.4 \pm 8.45 \times 10^{-4}$  trials;  
1519  $T(4.32 \times 10^3) = -15.26$ ,  $p = 3.11 \times 10^{-51}$ ) relative to the full model.

1520 D. In the likelihood-oscillation-only model, the smoothed probabilities of stimulus- and  
1521 history-congruence (sliding windows of  $\pm 5$  trials) fluctuated as a scale-invariant process with  
1522 a  $1/f$  power law, i.e., at power densities that were inversely proportional to the frequency  
1523 (power  $\sim 1/f^\beta$ ; stimulus-congruence:  $\beta = -0.81 \pm 1.17 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -688.65$ ,  $p$   
1524 <  $2.2 \times 10^{-308}$ ; history-congruence:  $\beta = -0.79 \pm 1.14 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -698.13$ ,  $p <$   
1525  $2.2 \times 10^{-308}$ ).

1526 E. In the likelihood-oscillation-only model, the distribution of phase shift between fluctuations  
1527 in simulated stimulus- and history-congruence peaked at half a cycle ( $\pi$  denoted by dotted  
1528 line). In contrast to the full model, the dynamic probabilities of simulated stimulus- and  
1529 history-congruence were positively correlated ( $\beta = 2.7 \times 10^{-3} \pm 7.6 \times 10^{-4}$ ,  $T(2.02 \times 10^6) =$   
1530  $3.55$ ,  $p = 3.8 \times 10^{-4}$ ).

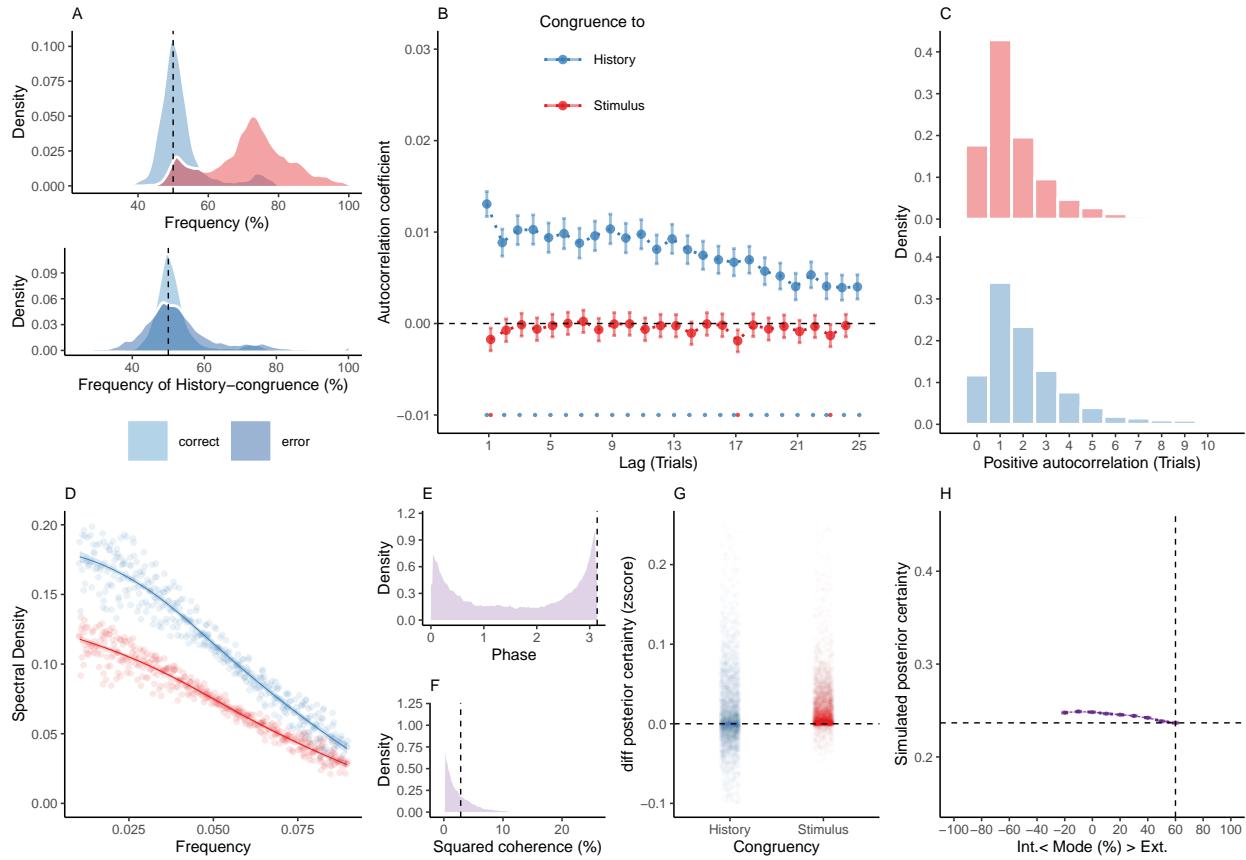
1531 F. In the likelihood-oscillation-only model, the average squared coherence between fluctuations  
1532 in simulated stimulus- and history-congruence (black dotted line) was reduced in comparison  
1533 to the full model ( $T(3.51 \times 10^3) = -4.56$ ,  $p = 5.27 \times 10^{-6}$ ) and amounted to  $3.43 \pm 1.02 \times 10^{-3}\%$ .

1534 G. Similar to the full bimodal inference model, confidence simulated from the likelihood-  
1535 oscillation-only model was enhanced for stimulus-congruent choices ( $\beta = 0.03 \pm 1.42 \times 10^{-4}$ ,

<sub>1536</sub>  $T(2.1 \times 10^6) = 191.78$ ,  $p < 2.2 \times 10^{-308}$ ) and history-congruent choices ( $\beta = 9.1 \times 10^{-3} \pm$   
<sub>1537</sub>  $1.25 \times 10^{-4}$ ,  $T(2.1 \times 10^6) = 72.51$ ,  $p < 2.2 \times 10^{-308}$ ).

<sub>1538</sub> H. In the likelihood-oscillation-only model, the positive quadratic relationship between the  
<sub>1539</sub> mode of perceptual processing and confidence was markedly reduced in comparison to the full  
<sub>1540</sub> model ( $\beta_2 = 0.34 \pm 0.1$ ,  $T(2.1 \times 10^6) = 3.49$ ,  $p = 4.78 \times 10^{-4}$ ). The horizontal and vertical  
<sub>1541</sub> dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1542 **9.15 Supplemental Figure S11**



1543 **Supplemental Figure S11. Reduced Control Model M3: Only oscillation of the prior.** When simulating data for the *prior-oscillation-only model*, we removed the oscillation from the prior term by setting the amplitude  $a_{LLR}$  to zero. Simulated data thus depended only on the participant-wise estimates for hazard rate  $H$ , amplitude  $a_\psi$ , frequency  $f$ , phase  $p$  and inverse decision temperature  $\zeta$ .

1544 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were  
 1545 stimulus-congruent in  $71.97\% \pm 0.17\%$  of trials (in red). History-congruent amounted to  
 1546  $52.1\% \pm 0.11\%$  of trials (in blue). As in the full model, the prior-oscillation-only showed a  
 1547 significant bias toward perceptual history  $T(4.32 \times 10^3) = 18.34$ ,  $p = 1.98 \times 10^{-72}$ ; upper  
 1548 panel). Similarly, history-congruent choices were more frequent at error trials ( $T(4.31 \times 10^3)$   
 1549  $= 12.35$ ,  $p = 1.88 \times 10^{-34}$ ; lower panel).

1550 B. In the prior-oscillation-only model, we did not observe any significant positive autocor-

<sub>1556</sub> relation of stimulus-congruence , whereas the autocorrelation of history-congruence was  
<sub>1557</sub> preserved.

<sub>1558</sub> C. In the prior-oscillation-only model, the number of consecutive trials at which true au-  
<sub>1559</sub> tocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted  
<sub>1560</sub> data did was decreased with respect to stimulus-congruence relative to the full model ( $1.8 \pm$   
<sub>1561</sub>  $1.01 \times 10^{-3}$  trials;  $T(4.31 \times 10^3) = -6.48$ ,  $p = 1.03 \times 10^{-10}$ ), but did not differ from the full  
<sub>1562</sub> model with respect to history-congruence ( $4.25 \pm 1.84 \times 10^{-3}$  trials;  $T(4.32 \times 10^3) = 0.07$ ,  $p$   
<sub>1563</sub> = 0.95).

<sub>1564</sub> D. In the prior-oscillation-only model, the smoothed probabilities of stimulus- and history-  
<sub>1565</sub> congruence (sliding windows of  $\pm 5$  trials) fluctuated as a scale-invariant process with a  $1/f$   
<sub>1566</sub> power law, i.e., at power densities that were inversely proportional to the frequency (power  
<sub>1567</sub>  $\sim 1/f^\beta$ ; stimulus-congruence:  $\beta = -0.78 \pm 1.11 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -706.62$ ,  $p <$   
<sub>1568</sub>  $2.2 \times 10^{-308}$ ; history-congruence:  $\beta = -0.83 \pm 1.27 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -651.6$ ,  $p <$   
<sub>1569</sub>  $2.2 \times 10^{-308}$ ).

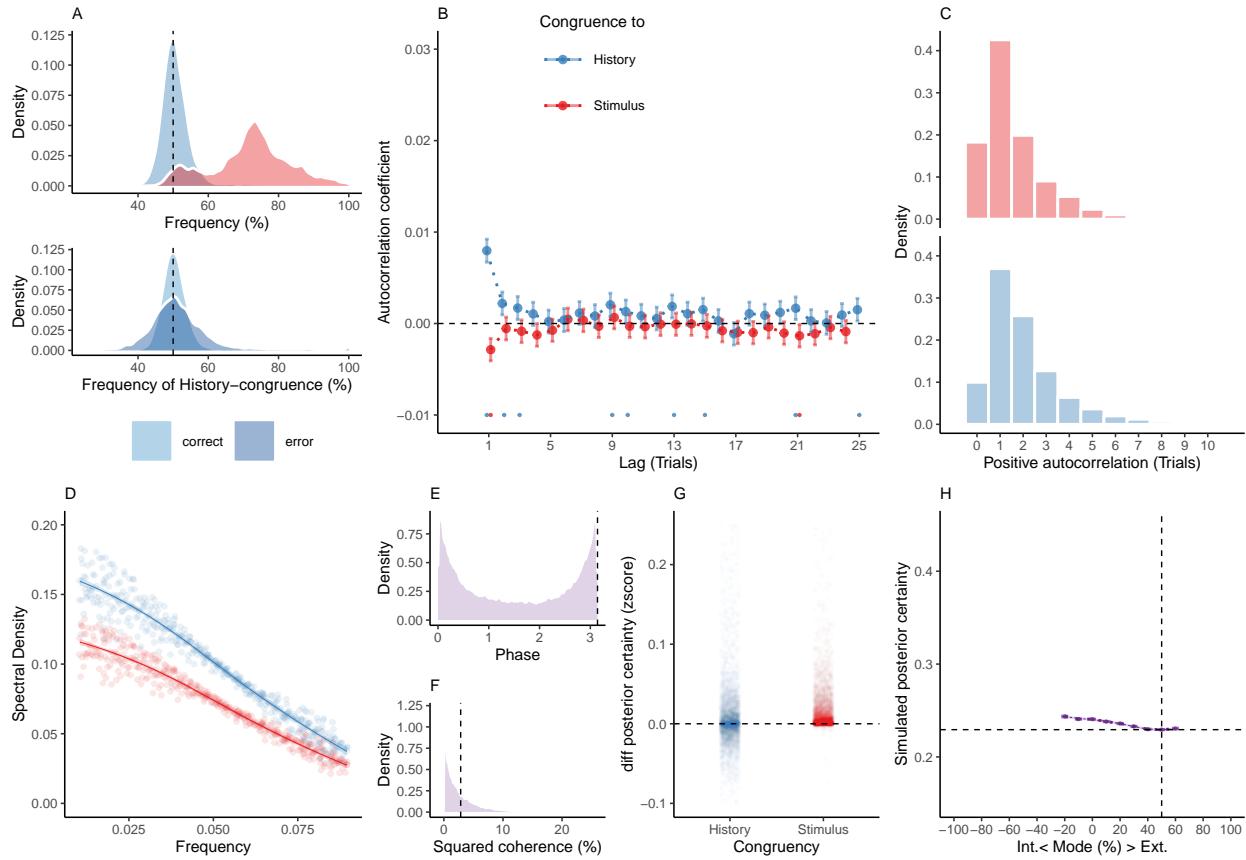
<sub>1570</sub> E. In the prior-oscillation-only model, the distribution of phase shift between fluctuations  
<sub>1571</sub> in simulated stimulus- and history-congruence peaked at half a cycle ( $\pi$  denoted by dotted  
<sub>1572</sub> line). Similar to the full model, the dynamic probabilities of simulated stimulus- and history-  
<sub>1573</sub> congruence were anti-correlated ( $\beta = -0.03 \pm 8.61 \times 10^{-4}$ ,  $T(2.12 \times 10^6) = -34.03$ ,  $p =$   
<sub>1574</sub>  $8.17 \times 10^{-254}$ ).

<sub>1575</sub> F. In the prior-oscillation-only model, the average squared coherence between fluctuations in  
<sub>1576</sub> simulated stimulus- and history-congruence (black dotted line) was reduced in comparison to  
<sub>1577</sub> the full model ( $T(3.54 \times 10^3) = -3.22$ ,  $p = 1.28 \times 10^{-3}$ ) and amounted to  $3.52 \pm 1.04 \times 10^{-3}\%$ .

<sub>1578</sub> G. Similar to the full bimodal inference model, confidence simulated from the prior-oscillation-  
<sub>1579</sub> only model was enhanced for stimulus-congruent choices ( $\beta = 0.02 \pm 1.44 \times 10^{-4}$ ,  $T(2.03 \times 10^6)$   
<sub>1580</sub> = 128.53,  $p < 2.2 \times 10^{-308}$ ) and history-congruent choices ( $\beta = 0.01 \pm 1.26 \times 10^{-4}$ ,  $T(2.03 \times 10^6)$   
<sub>1581</sub> = 88.24,  $p < 2.2 \times 10^{-308}$ ).

<sub>1582</sub> H. In contrast to the full bimodal inference model, the prior-oscillation-only model did  
<sub>1583</sub> not yield a positive quadratic relationship between the mode of perceptual processing and  
<sub>1584</sub> confidence ( $\beta_2 = -0.17 \pm 0.1$ ,  $T(2.04 \times 10^6) = -1.66$ ,  $p = 0.1$ ). The horizontal and vertical  
<sub>1585</sub> dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1586 **9.16 Supplemental Figure S12**



1587 **1588 Supplemental Figure S12. Reduced Control Model M4: Normative evidence**

1589 **accumulation.** When simulating data for the *normative-evidence-accumulation model*, we  
 1590 removed the oscillation from the likelihood and prior terms by setting the amplitudes  $a_{LLR}$   
 1591 and  $a_\psi$  to zero. Simulated data thus depended only on the participant-wise estimates for  
 1592 hazard rate  $H$  and inverse decision temperature  $\zeta$ .

1593 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were  
 1594 stimulus-congruent in  $71.97\% \pm 0.17\%$  of trials (in red). History-congruent amounted to  
 1595  $50.73\% \pm 0.07\%$  of trials (in blue). As in the full model, the no-oscillation model showed  
 1596 a significant bias toward perceptual history  $T(4.32 \times 10^3) = 9.94$ ,  $p = 4.88 \times 10^{-23}$ ; upper  
 1597 panel). Similarly, history-congruent choices were more frequent at error trials ( $T(4.31 \times 10^3)$   
 1598  $= 10.59$ ,  $p = 7.02 \times 10^{-26}$ ; lower panel).

1599 B. In the normative-evidence-accumulation model, we did not find significant autocor-

<sub>1600</sub> relations for stimulus-congruence. Likewise, we did not observe any autocorrelation of  
<sub>1601</sub> history-congruence beyond the first three consecutive trials.

<sub>1602</sub> C. In the normative-evidence-accumulation model, the number of consecutive trials at  
<sub>1603</sub> which true autocorrelation coefficients exceeded the autocorrelation coefficients for randomly  
<sub>1604</sub> permuted data decreased with respect to both stimulus-congruence ( $1.8 \pm 1.59 \times 10^{-3}$  trials;  
<sub>1605</sub>  $T(4.31 \times 10^3) = -5.21$ ,  $p = 2 \times 10^{-7}$ ) and history-congruence ( $2.18 \pm 5.48 \times 10^{-4}$  trials;  
<sub>1606</sub>  $T(4.32 \times 10^3) = -17.1$ ,  $p = 1.75 \times 10^{-63}$ ) relative to the full model.

<sub>1607</sub> D. In the normative-evidence-accumulation model, the smoothed probabilities of stimulus-  
<sub>1608</sub> and history-congruence (sliding windows of  $\pm 5$  trials) fluctuated as a scale-invariant process  
<sub>1609</sub> with a  $1/f$  power law, i.e., at power densities that were inversely proportional to the frequency  
<sub>1610</sub> (power  $\sim 1/f^\beta$ ; stimulus-congruence:  $\beta = -0.78 \pm 1.1 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -706.93$ ,  $p <$   
<sub>1611</sub>  $2.2 \times 10^{-308}$ ; history-congruence:  $\beta = -0.79 \pm 1.12 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -702.46$ ,  $p <$   
<sub>1612</sub>  $2.2 \times 10^{-308}$ ).

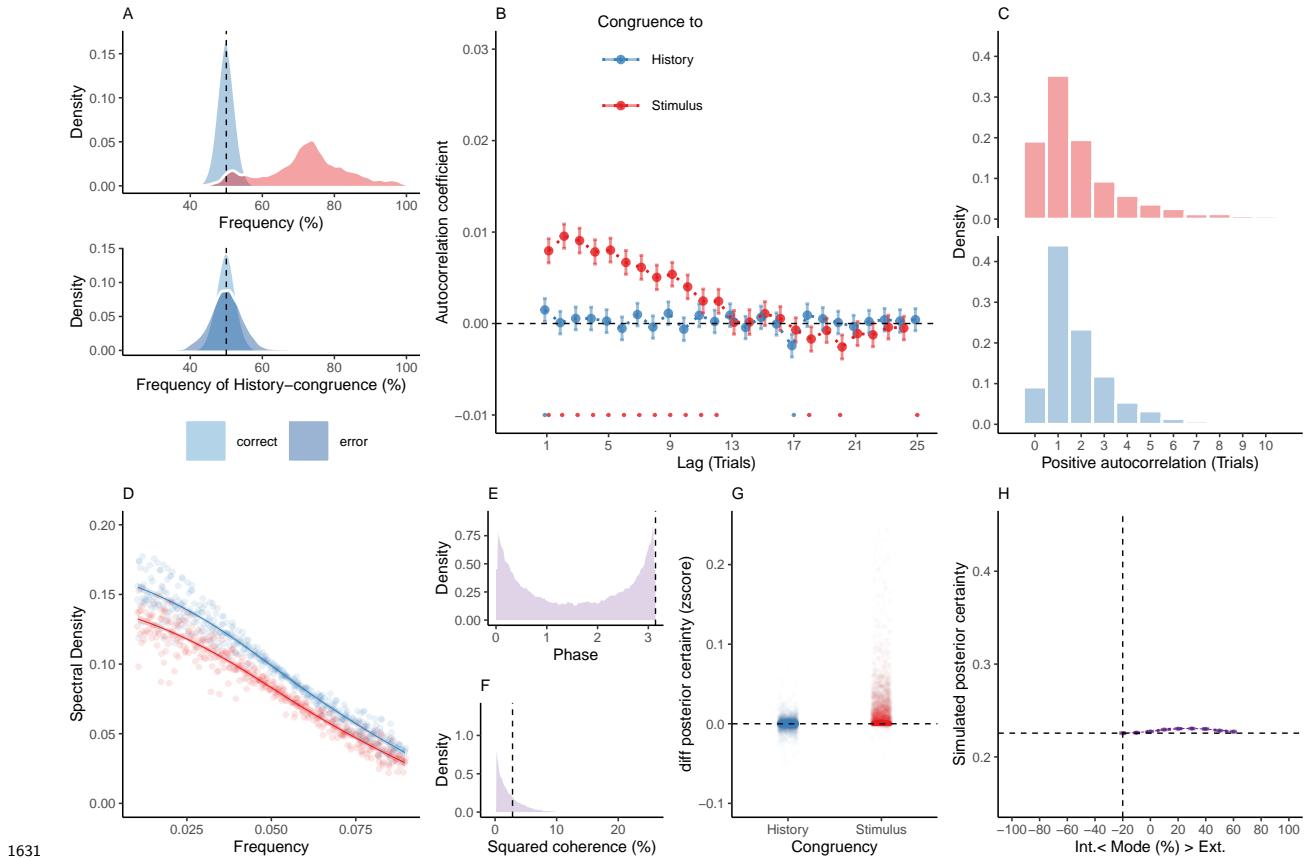
<sub>1613</sub> E. In the normative-evidence-accumulation model, the distribution of phase shift between  
<sub>1614</sub> fluctuations in simulated stimulus- and history-congruence peaked at half a cycle ( $\pi$  denoted  
<sub>1615</sub> by dotted line). In contrast to the full model, the dynamic probabilities of simulated stimulus-  
<sub>1616</sub> and history-congruence were positively correlated ( $\beta = 4.3 \times 10^{-3} \pm 7.97 \times 10^{-4}$ ,  $T(1.98 \times 10^6)$   
<sub>1617</sub>  $= 5.4$ ,  $p = 6.59 \times 10^{-8}$ ).

<sub>1618</sub> F. In the normative-evidence-accumulation model, the average squared coherence between  
<sub>1619</sub> fluctuations in simulated stimulus- and history-congruence (black dotted line) was reduced in  
<sub>1620</sub> comparison to the full model ( $T(3.52 \times 10^3) = -6.27$ ,  $p = 3.97 \times 10^{-10}$ ) and amounted to  
<sub>1621</sub>  $3.26 \pm 8.88 \times 10^{-4}\%$ .

<sub>1622</sub> G. Similar to the full bimodal inference model, confidence simulated from the no-oscillation  
<sub>1623</sub> model was enhanced for stimulus-congruent choices ( $\beta = 0.01 \pm 1.05 \times 10^{-4}$ ,  $T(2.1 \times 10^6)$   
<sub>1624</sub>  $= 139.17$ ,  $p < 2.2 \times 10^{-308}$ ) and history-congruent choices ( $\beta = 8.05 \times 10^{-3} \pm 9.2 \times 10^{-5}$ ,  
<sub>1625</sub>  $T(2.1 \times 10^6) = 87.54$ ,  $p < 2.2 \times 10^{-308}$ ).

<sub>1626</sub> H. In the normative-evidence-accumulation model, the positive quadratic relationship between  
<sub>1627</sub> the mode of perceptual processing and confidence was markedly reduced in comparison to  
<sub>1628</sub> the full model ( $\beta_2 = 0.14 \pm 0.07$ ,  $T(2.1 \times 10^6) = 1.95$ ,  $p = 0.05$ ). The horizontal and vertical  
<sub>1629</sub> dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1630 **9.17 Supplemental Figure S13**



1632 **Supplemental Figure S13. Reduced Control Model M5: No accumulation of**

1633 **information across trials.** When simulating data for the *no-evidence-accumulation model*,

1634 we removed the accumulation of information across trials by setting the Hazard rate  $H$  to

1635 0.5. Simulated data thus depended only on the participant-wise estimates for the amplitudes

1636  $a_{LLR/\psi}$ , frequency  $f$ , phase  $p$  and inverse decision temperature  $\zeta$ .

1637 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were

1638 stimulus-congruent in  $72.14\% \pm 0.17\%$  of trials (in red). History-congruent amounted to

1639  $49.89\% \pm 0.03\%$  of trials (in blue). In contrast to the full model, the no-accumulation model

1640 showed a significant bias against perceptual history  $T(4.32 \times 10^3) = -3.28$ ,  $p = 1.06 \times 10^{-3}$ ;

1641 upper panel). In contrast to the full model, there was no difference in the frequency of

1642 history-congruent choices between correct and error trials ( $T(4.31 \times 10^3) = 0.76$ ,  $p = 0.44$ ;

1643 lower panel).

<sub>1644</sub> B. In the no-evidence-accumulation model, we found no significant autocorrelation of history-  
<sub>1645</sub> congruence beyond the first trial, whereas the autocorrelation of stimulus-congruence was  
<sub>1646</sub> preserved.

<sub>1647</sub> C. In the no-evidence-accumulation model, the number of consecutive trials at which true  
<sub>1648</sub> autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted  
<sub>1649</sub> data increased with respect to stimulus-congruence ( $2.83 \pm 1.49 \times 10^{-3}$  trials;  $T(4.31 \times 10^3) =$   
<sub>1650</sub>  $3.45$ ,  $p = 5.73 \times 10^{-4}$ ) and decreased with respect to history-congruence ( $1.85 \pm 3.49 \times 10^{-4}$   
<sub>1651</sub> trials;  $T(4.32 \times 10^3) = -19.37$ ,  $p = 3.49 \times 10^{-80}$ ) relative to the full model.

<sub>1652</sub> D. In the no-evidence-accumulation model, the smoothed probabilities of stimulus- and  
<sub>1653</sub> history-congruence (sliding windows of  $\pm 5$  trials) fluctuated as a scale-invariant process with  
<sub>1654</sub> a  $1/f$  power law, i.e., at power densities that were inversely proportional to the frequency  
<sub>1655</sub> (power  $\sim 1/f^\beta$ ; stimulus-congruence:  $\beta = -0.82 \pm 1.2 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -681.98$ ,  $p <$   
<sub>1656</sub>  $2.2 \times 10^{-308}$ ; history-congruence:  $\beta = -0.78 \pm 1.11 \times 10^{-3}$ ,  $T(1.92 \times 10^5) = -706.57$ ,  $p <$   
<sub>1657</sub>  $2.2 \times 10^{-308}$ ).

<sub>1658</sub> E. In the no-evidence-accumulation model, the distribution of phase shift between fluctuations  
<sub>1659</sub> in simulated stimulus- and history-congruence peaked at half a cycle ( $\pi$  denoted by dotted  
<sub>1660</sub> line). In contrast to the full model, the dynamic probabilities of simulated stimulus- and  
<sub>1661</sub> history-congruence were not significantly anti-correlated ( $\beta = 6.39 \times 10^{-4} \pm 7.22 \times 10^{-4}$ ,  
<sub>1662</sub>  $T(8.89 \times 10^5) = 0.89$ ,  $p = 0.38$ ).

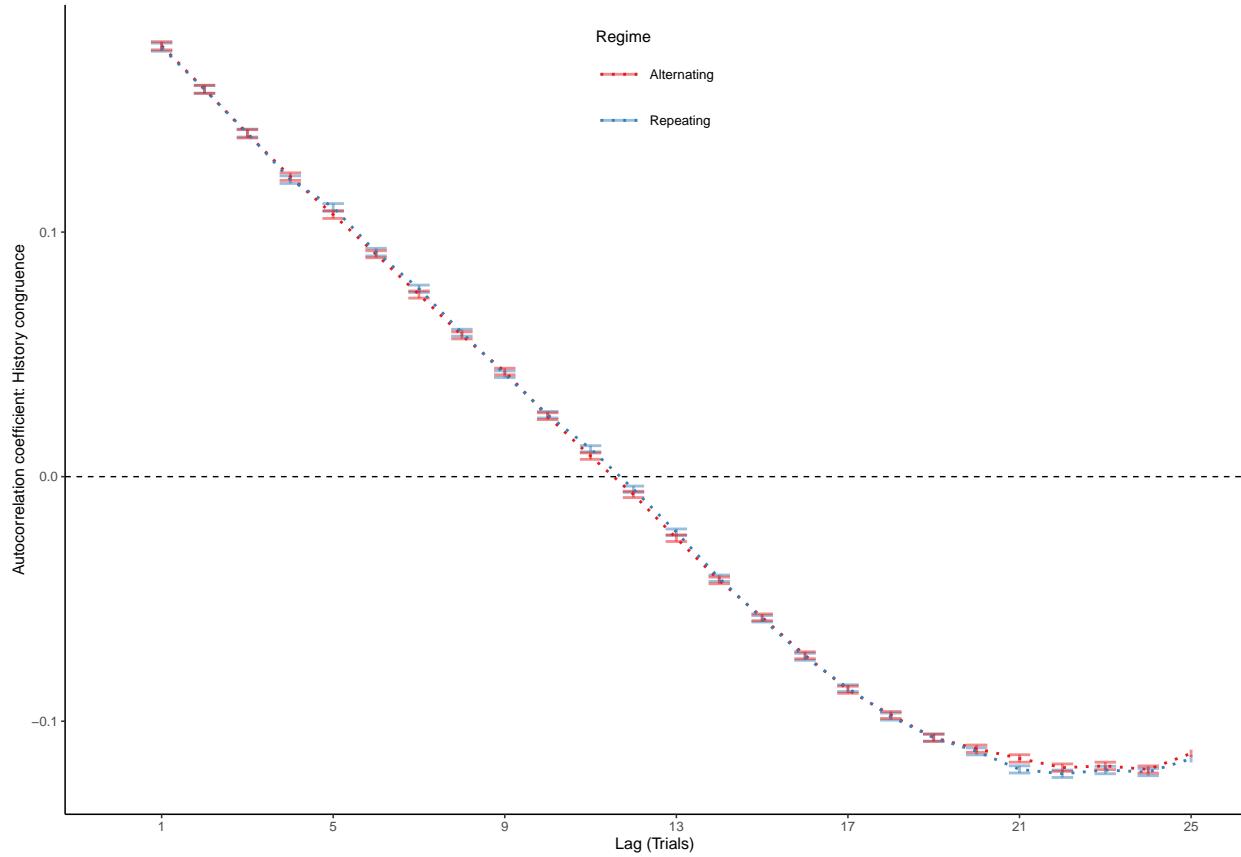
<sub>1663</sub> F. In the no-evidence-accumulation model, the average squared coherence between fluctuations  
<sub>1664</sub> in simulated stimulus- and history-congruence (black dotted line) was reduced in comparison  
<sub>1665</sub> to the full model ( $T(3.56 \times 10^3) = -9.96$ ,  $p = 4.63 \times 10^{-23}$ ) and amounted to  $2.8 \pm 7.29 \times 10^{-4}\%$ .

<sub>1666</sub> G. Similar to the full bimodal inference model, confidence simulated from the no-evidence-  
<sub>1667</sub> accumulation model was enhanced for stimulus-congruent choices ( $\beta = 0.01 \pm 9.4 \times 10^{-5}$ ,  
<sub>1668</sub>  $T(2.11 \times 10^6) = 158.1$ ,  $p < 2.2 \times 10^{-308}$ ). In contrast to the full bimodal inference model,  
<sub>1669</sub> history-congruent choices were not characterized by enhanced confidence ( $\beta = 8.78 \times 10^{-5} \pm$

<sub>1670</sub>  $8.21 \times 10^{-5}$ ,  $T(2.11 \times 10^6) = 1.07$ ,  $p = 0.29$ ).

<sub>1671</sub> H. In the no-evidence-accumulation model, the positive quadratic relationship between the  
<sub>1672</sub> mode of perceptual processing and confidence was markedly reduced in comparison to the full  
<sub>1673</sub> model ( $\beta_2 = 0.19 \pm 0.06$ ,  $T(2.11 \times 10^6) = 3$ ,  $p = 2.69 \times 10^{-3}$ ). The horizontal and vertical  
<sub>1674</sub> dotted lines indicate minimum posterior certainty and the associated mode, respectively.

<sup>1675</sup> **9.18 Supplemental Figure S14**



<sup>1676</sup> **Supplemental Figure S14. Autocorrelation of history-congruence of alternating**  
<sup>1677</sup> **and repeating biases.** Here, we simulate the autocorrelation of history-congruence in  $10^3$   
<sup>1678</sup> synthetic participants. In the repeating regime (blue), history-congruence fluctuated between  
<sup>1679</sup> 50% and 80% (blue) in interleaved blocks (10 blocks per condition with a random duration  
<sup>1680</sup> between 15 and 30 trials). In the alternation regime (red), history-congruence fluctuated  
<sup>1681</sup> between 50% and 20%. The resulting autocorrelation curves for history-congruence overlap,  
<sup>1682</sup> indicating that our analysis is able to accommodate both repeating and alternating biases.  
<sup>1683</sup>

1684 9.19 Supplemental Table T1

Authors	Journal	Year
Bang, Shekhar, Rahnev	JEP:General	2019
Bang, Shekhar, Rahnev	JEP:General	2019
Calder-Travis, Charles, Bogacz, Yeung	Unpublished	NA
Clark & Merfeld	Journal of Neurophysiology	2018
Clark	Unpublished	NA
Faivre, Filevich, Solovey, Kuhn, Blanke	Journal of Neuroscience	2018
Faivre, Vuillaume, Blanke, Cleeremans	bioRxiv	2018
Filevich & Fandakova	Unplublished	NA
Gajdos, Fleming, Saez Garcia, Weindel, Davranche	Neuroscience of Consciousness	2019
Gherman & Philiastides	eLife	2018
Haddara & Rahnev	PsyArXiv	2020
Haddara & Rahnev	PsyArXiv	2020
Hainguerlot, Vergnaud, & de Gardelle	Scientific Reports	2018
Hainguerlot, Gajdos, Vergnaud, & de Gardelle	Unpublished	NA
Jachs, Blanco, Grantham-Hill, Soto	JEP:HPP	2015
Jachs, Blanco, Grantham-Hill, Soto	JEP:HPP	2015
Jachs, Blanco, Grantham-Hill, Soto	JEP:HPP	2015
Jaquiere, Yeung	Unpublished	NA
Kvam, Pleskac, Yu, Busemeyer	PNAS	2015
Kvam, Pleskac, Yu, Busemeyer	PNAS	2015
Kvam and Pleskac	Cognition	2016
Law, Lee	Unpublished	NA
Lebreton, et al.	Sci. Advances	2018
Lempert, Chen, & Fleming	PlosOne	2015
Locke*, Gaffin-Cahn*, Hosseiniaveh, Mamassian, & Landy	Attention, Perception, & Psychophysics	2020
Maniscalco, McCurdy,Odegaard, & Lau	J Neurosci	2017
Maniscalco, McCurdy,Odegaard, & Lau	J Neurosci	2017
Maniscalco, McCurdy,Odegaard, & Lau	J Neurosci	2017
Maniscalco, McCurdy,Odegaard, & Lau	J Neurosci	2017
Martin, Hsu	Unpublished	NA
Massoni & Roux	Journal of Mathematical Psychology	2017
Massoni	Unpublished	NA
Mazor, Friston & Fleming	eLife	2020
Mei, Rankine,Olafsson, Soto	bioRxiv	2019
Mei, Rankine,Olafsson, Soto	bioRxiv	2019
O'Hora, Zgonnikov, Kenny, Wong-Lin	Fechner Day proceedings	2017
O'Hora, Zgonnikov, CiChocki	Unpublished	NA

(continued)

Authors	Journal	Year
O'Hora, Zgonnikov, Neverauskaite	Unpublished	NA
Palser et al	Consciousness & Cognition	2018
Pereira, Faivre, Iturrate et al.	bioRxiv	2018
Prieto et al.	Submitted	NA
Rahnev et al	J Neurophysiol	2013
Rausch & Zehetleitner	Front Psychol	2016
Rausch et al	Attention, Perception, & Psychophysics	2018
Rausch et al	Attention, Perception, & Psychophysics	2018
Rausch, Zehetleitner, Steinhauser, & Maier	NeuroImage	2020
Recht, de Gardelle & Mamassian	Unpublished	NA
Reyes et al.	PlosOne	2015
Reyes et al.	Submitted	NA
Rouault, Seow, Gillan, Fleming	Biol. Psychiatry	2018
Rouault, Seow, Gillan, Fleming	Biol. Psychiatry	2018
Rouault, Dayan, Fleming	Nat Commun	2019
Sadeghi et al	Scientific Reports	2017
Schmidt et al.	Consc Cog	2019
Shekhar & Rahnev	J Neuroscience	2018
Shekhar & Rahnev	PsyArXiv	2020
Sherman et al	Journal of Neuroscience	2016
Sherman et al	Journal of Cognitive Neuroscience	2016
Sherman et al	Unpublished	NA
Sherman et al	Unpublished	NA
Siedlecka, Wereszczyski, Paulewicz, Wierzchon	bioRxiv	2019
Song et al	Consciousness & Cognition	2011
van Boxtel, Orchard, Tsuchiya	bioRxiv	2019
van Boxtel, Orchard, Tsuchiya	bioRxiv	2019
Wierzchon, Paulewicz, Asanowicz, Timmermans & Cleeremans	Consciousness and Cognition	2014
Wierzchon, Anzulewicz, Hobot, Paulewicz & Sackur	Consciousness and Cognition	2019

<sub>1685</sub> **9.20 Supplemental Table T2**

Parameters	Interpretation
$\alpha$	Sensitivity to sensory information
H	Expected probability of a switch in the cause of sensory information (Hazard)
$a_{LLR}$	Amplitude of fluctuations in likelihood precision $\omega_{LLR}$
$a_\psi$	Amplitude of fluctuations in prior precision $\omega_\psi$
f	Frequency of $\omega_{LLR}$ and $\omega_\psi$
p	Phase (p for $\omega_{LLR}$ ; p + $\pi$ for $\omega_\psi$ )
$\zeta$	Inverse decision temperature

1686 10 Response to Reviewers

1687 10.1 Reviewer 1

1688 This was an interesting and thought-provoking submission. I note that it is  
1689 a revision: I am therefore supposing that the authors have already responded  
1690 to one round of reviewer comments and that you are potentially interested in  
1691 publishing this work. In brief, I think there are many elements of this report that  
1692 warrant publication; however, there are some parts that are less compelling and  
1693 could be deferred to a subsequent paper. The paper is far too long and would  
1694 benefit greatly from being streamlined. Furthermore, some of the modeling is  
1695 overengineered and is difficult to follow. I have tried to suggest how the authors  
1696 might improve the presentation of their work in my comments to authors.

1697 I enjoyed reading this long but thought-provoking report of fluctuations in the  
1698 sensitivity to sensory evidence in perceptual decision-making tasks. There were  
1699 some parts of this report that were compelling and interesting. Other parts were  
1700 less convincing and difficult to understand. Overall, this paper is far too long. An  
1701 analogy that might help here is that a dinner guest is very entertaining for the  
1702 first hour or so - and then overstays their welcome; until you start wishing they  
1703 would leave. Another analogy, which came to mind, was that the modeling—and  
1704 its interpretation—was a bit autistic (i.e., lots of fascinating if questionable detail  
1705 with a lack of central coherence).

1706 I think that both issues could be resolved by shortening the paper and removing  
1707 (or, at least, greatly simplifying) the final simulation studies of metacognition. I  
1708 try to unpack this suggestion in the following.

1709 We would like to thank Prof. Friston for the very insightful and helpful comments on our  
1710 manuscript. We fully agree that our ideas about the computational function of between-mode

1711 fluctuations and the associated simulations may be presented in a more accessible form in a  
1712 standalone paper. As we outlined in more detail below, we have streamlined our findings  
1713 and rewrote the paper and reduced it's length by shortening the sections on computational  
1714 modeling. We have also followed Prof. Friston's suggestion to interpret the effects of mode  
1715 on RT and confidence in the context of predictive processing definitions of attention, namely  
1716 the allocation of precision between prior and likelihood.

1717 **Major points:**

1718 **As I understand it, you have used publicly available data on perceptual decision-**  
1719 **making to demonstrate slow fluctuations in the tendency to predicate perceptual**  
1720 **decisions on the stimuli and on the history of recent decisions. You find scale-free**  
1721 **fluctuations in this tendency — that are anti-correlated — and interpret this as**  
1722 **fluctuations in the precision afforded sensory evidence, relative to prior beliefs.**  
1723 **This interpretation is based upon a model of serial dependencies (parameterised**  
1724 **with a hazard function).**

1725 **The stimulus and history (i.e., likelihood and prior) sensitivities are anti-correlated**  
1726 **and both show scale free behavior. This is reproduced in men and mice. You**  
1727 **then proceed to model this with periodic fluctuations in the precisions or weights**  
1728 **applied to the likelihood and prior that are in anti-phase - and then estimate the**  
1729 **parameters of the ensuing model. Finally, you then simulate the learning of the**  
1730 **hazard parameter — and something called metacognition - to show that periodic**  
1731 **fluctuations improve estimates of metacognition (based upon a Rescorla-Wagner**  
1732 **model of learning). You motivate this by suggesting that the fluctuations in**  
1733 **sensitivity are somehow necessary to elude circular inference and provide better**  
1734 **estimates of precision.**

1735 **Note that I am reading the parameters omega\_LL and omega\_psi as the**  
1736 **precision of the likelihood and prior, where the precision of the likelihood is**

1737 called sensory precision. This contrasts with your use of sensory precision, which  
1738 seems to be attributed to a metacognitive construct M.

1739 As noted above, all of this is fascinating but there are too many moving parts  
1740 that do not fit together comfortably. I will list a few examples:

1741 **10.1.1 Comment 1**

1742 If, empirically, the fluctuations in sensitivity are scale-free with a 1/f power law,  
1743 why did you elect to model fluctuations in precision as a periodic function with  
1744 one unique timescale (i.e., f).?

1745 The reason for choosing a unique timescale  $f$  was to enable our model to depict the dominant  
1746 timescale at which prior and likelihood precision fluctuate in their impact on perceptual  
1747 decision-making, giving rise to between-mode fluctuations. We think that identifying this  
1748 timescale is important for planning future experiments targeted at between-mode fluctuations  
1749 and their manipulation by causal interventions (e.g., pharmacology or TMS). The posterior  
1750 value for  $f$  lies at approximately  $0.11 \frac{1}{N_{trials}}$  in both humans and mice. The value of  $f$   
1751 approximately matches the transition probabilities between *engaged* and *disengaged* states in  
1752 work assessing fluctuations in perceptual decision-making using Hidden Markov models (stay  
1753 probabilities ranged between 0.94 and 0.98, see Ashwood et al., Nature Neuroscience 2022).  
1754 Simulating from our model (Figure 4) replicates the 1/f feature of the empirical data. Please  
1755 note that the individual trial is the smallest unit of *measurement* for these fluctuations, such  
1756 that our analysis is limited by definition to frequencies below 1 ( $1/N_{trials}$ ).

1757 We now provide a rationale for choosing one value for  $f$  - identifying the dominant timescale  
1758 for fluctuations in mode - in the results section:

- 1759 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-  
1760 biased modes of perceptual processing that occur irrespective of the sequence of preceding  
1761 experiences, we assumed that likelihood and prior vary in their influence on the perceptual

1762 decision according to fluctuations governed by  $\omega_{LLR}$  and  $\omega_\psi$ . These anti-phase sine  
1763 functions (defined by amplitudes  $a_{LLR/\psi}$ , frequency  $f$  and phase  $p$ ) determine the  
1764 precision afforded to the likelihood and prior<sup>53</sup>. The implicit anti-phase fluctuations  
1765 are mandated by Bayes-optimal formulations in which inference depends only on the  
1766 relative values of prior and likelihood precision (i.e., the Kalman gain<sup>54</sup>). As such,  $\omega_{LLR}$   
1767 and  $\omega_\psi$  implement a hyperprior<sup>55</sup> in which the likelihood and prior precisions are shifted  
1768 against each other at a dominant timescale defined by  $f$ : (...)

- 1769 • (...) The parameter  $f$  captures the dominant time scale at which likelihood (amplitude  
1770 humans:  $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$ ; mice:  $a_{LLR} = 0.39 \pm 1.08 \times 10^{-3}$  and prior precision  
1771 (amplitude humans:  $a_\psi = 1.44 \pm 5.27 \times 10^{-4}$ ; mice:  $a_\psi = 1.71 \pm 7.15 \times 10^{-3}$  were shifted  
1772 against each other and was estimated at  $0.11 \pm 1.68 \times 10^{-5} 1/N_{trials}$  and  $0.11 \pm 1.63 \times 10^{-4}$   
1773  $1/N_{trials}$  in mice.
- 1774 • Table 2 (see response to Comment 22 by Reviewer 1) contains an additional definition  
1775 for all model parameters, including  $f$ .

### 1776 10.1.2 Comment 2

1777 **At present, the estimates of meta-cognition (M) play the role of accumulated  
1778 estimates of (sensory or prior) precision. Why are these not used in your model  
1779 of perceptual decisions in Equation 2.**

1780 In our model, the parameter  $\alpha$  controls the encoding precision by governing the transformation  
1781 from sensory stimuli to the log likelihood ratio (LLR) via the equations (13-16) (the LLR  
1782 ends up closer to zero when  $\alpha$  is low). Our simulations on the adaptive benefits of bimodal  
1783 inference rest on the assumption that  $\alpha$  may change unpredictably. The construct  $M$  is a  
1784 belief about  $\alpha$  that may be useful for, e.g., communicating the precision of sensory encoding  
1785 to other cognitive domains or agents. To our mind,  $\alpha$  is a feature of low-level sensory encoding  
1786 that cannot be modulated by top-down beliefs such as  $M$ . This is why we did not include

<sub>1787</sub>  $M$  in equation (2). Please note that we have removed this section following Comment 9 of  
<sub>1788</sub> Reviewer 1.

<sub>1789</sub> **10.1.3 Comment 3**

<sub>1790</sub> **Why do you assume that non-specific increases in attention and arousal will**  
<sub>1791</sub> **increase reaction times? If one has very precise prior beliefs (and is not attending**  
<sub>1792</sub> **to stimuli), would you not expect a decrease in reaction time?**

<sub>1793</sub> Thanks a lot for pointing this out (see also the Comment below and Comment 6 by Reviewer  
<sub>1794</sub> 3). Both high prior and high likelihood precision lead to higher absolute values of the log  
<sub>1795</sub> posterior ratio (reflecting certainty encoded by the decision variable), and thus faster RTs.  
<sub>1796</sub> This is reflected empirically by RTs in humans (Figure 2) and to a lesser degree in mice  
<sub>1797</sub> (Figure 3): RTs tended to be shorter for stronger biases toward both external and internal  
<sub>1798</sub> mode. Our model, which incorporates (i), the accumulation of information across trials, and  
<sub>1799</sub> (ii), fluctuations in the likelihood precision relative to the prior precision, recapitulates this  
<sub>1800</sub> feature of the data, which is lost or greatly attenuated when eliminating process (i) and/or  
<sub>1801</sub> (ii) (see model comparison and simulations below). Our data thus confirm the hypothesis  
<sub>1802</sub> that both high prior and likelihood precision lead to faster RTs.

<sub>1803</sub> In the previous version of the manuscript, we had included the relation between mode and  
<sub>1804</sub> RTs and confidence primarily as a defensive analysis against the proposition that what we  
<sub>1805</sub> call between-mode fluctuations is not a perceptual phenomenon, but occurs downstream of  
<sub>1806</sub> perception. One may imagine that fluctuations in perceptual performance are not influenced  
<sub>1807</sub> by periods of relative increases in prior precision (which decrease performance in fully  
<sub>1808</sub> randomized designs), but by periods when participants do not attend to the task at all, i.e.,  
<sub>1809</sub> neither to sensory information nor to prior precision. We propose that the analyses of RTs  
<sub>1810</sub> and confidence can give some insight into whether such alternative mechanisms may be at  
<sub>1811</sub> play, as we would assume longer RTs and lower confidence if participants failed to attend to  
<sub>1812</sub> the task at all.

1813 That being said, we realize that, due to the potential non-linearity in their relation to arousal  
1814 (see also Comment 6 by Reviewer 3), RTs and confidence cannot provide a definitive map  
1815 of where fluctuations in mode are situated in relation to arousal. Such a delineation may  
1816 potentially be provided by tracking of pupil size, response behavior or by neural data (e.g.,  
1817 noise correlations of fluctuations in LFP). These data are not available for the studies in  
1818 the Confidence Database, but were very recently published for the IBL database (after this  
1819 manuscript was submitted). While we believe that this is beyond the scope of this manuscript,  
1820 we will assess the relation of pupil diameter, motor behavior (turning of the response wheel)  
1821 and LFPs to between-mode fluctuations in a future publication using the IBL dataset.

1822 In light of the considerations above and our response to Comment 6 by Reviewer 3, we now  
1823 refer to attention in the predictive processing sense. We use the term “task engagement”  
1824 instead of “on-task attention” to refer to situation in which participants may not attend to  
1825 the task at all, e.g. due to low arousal or fatigue, and discuss these as alternative explanations  
1826 for between-mode fluctuations. We have made three sets of changes to our manuscript:

1827 First, we present our results on the relation of mode to RT and Confidence in a more  
1828 descriptive way, and do not use it as a strong defensive analysis against arousal:

1829 • The above results point to systematic fluctuations in the *decision variable*<sup>44</sup> that deter-  
1830 mines perceptual choices, causing enhanced sensitivity to external stimulus information  
1831 during external mode and increased biases toward preceding choices during internal  
1832 mode. As such, fluctuations in mode should influence downstream aspects of behavior  
1833 and cognition that operate on the perceptual decision variable<sup>44</sup>. To test this hypothesis  
1834 with respect to motor behavior and metacognition, we asked how bimodal inference  
1835 relates to response times (RTs) and confidence reports. (...)

1836 • (...) In sum, the above results indicate that reporting behavior and metacognition do  
1837 not map linearly onto the mode of sensory processing. Rather, they suggest that slow  
1838 fluctuations in the respective impact of external and internal information are most likely

1839 to affect perception at an early level of sensory analysis<sup>46,47</sup>. Such low-level processing  
1840 may thus integrate perceptual history with external inputs into a decision variable<sup>44</sup>  
1841 that influences not only perceptual choices, but also the speed and confidence at which  
1842 they are made.

- 1843 • In what follows, we probe alternative explanations for between-mode fluctuations, test  
1844 for the existence of modes in mice, and propose a predictive processing model that  
1845 explains fluctuations in mode by ongoing shifts in the precision afforded to external  
1846 sensory information relative to internal predictions driven by perceptual history.

1847 Second, we have re-written our discussion of the quadratic relationship of mode to RTs  
1848 and Confidence, focusing on predictive processing models of attention: - As a functional  
1849 explanation for bimodal inference, we propose that perception temporarily disengages from  
1850 internal predictions to form stable inferences about the statistical properties of the sensory  
1851 environment. Between-mode fluctuations may thus elude circular inferences that occur when  
1852 both the causes and the encoding of sensory stimuli are volatile<sup>19,57</sup>. By the same token, we  
1853 suggest that fluctuations in mode occur at the level of perceptual processing<sup>26,30,46,47</sup>, and are  
1854 not a passive phenomenon that is primarily driven by factors situated up- or downstream of  
1855 sensory analysis.

- 1856 • How does attention relate to between-mode fluctuations? According to predictive  
1857 processing, attention corresponds to the precision afforded to the probability distributions  
1858 that underlie perceptual inference<sup>53</sup>. From this perspective, fluctuations between external  
1859 and internal mode can be understood as ongoing shifts in the attention afforded to either  
1860 external sensory information (regulated via likelihood precision) or internal predictions  
1861 (regulated via prior precision). When the precision of either likelihood or prior increases,  
1862 posterior precision increases, which leads to faster RTs and higher confidence. Therefore,  
1863 when defined from the perspective of predictive processing as the precision afforded to

1864 likelihood and prior<sup>53</sup>, fluctuations in attention may provide a plausible explanation for  
1865 the quadratic relationship of mode to RTs and confidence (Figure 2H and J; Figure 3I;  
1866 Figure 3I).

1867 Third, we have added a more general discussion of our findings in the light of fluctuations in  
1868 task engagement:

1869 • Outside of the predictive processing field, attention is often understood in the context of  
1870 task engagement<sup>63</sup>, which varies according to the availability of cognitive resources that  
1871 are modulated by factors such as tonic arousal, familiarity with the task, or fatigue<sup>63</sup>. Our  
1872 results suggest that internal mode processing cannot be completely reduced to intervals  
1873 of low task engagement: In addition to shorter RTs and elevated confidence, choices  
1874 during internal mode were not random or globally biased, but driven by perceptual  
1875 history (Supplemental Figures S6-7). Moreover, our computational model identified  
1876 the dominant timescale of between-mode fluctuations at  $0.11\sqrt{1/N_{trials}}$ , which may be  
1877 compatible with fluctuations in arousal<sup>64</sup>, but is faster than to be expected for the  
1878 development of task familiarity or fatigue.

1879 • However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,  
1880 speed of response and confidence, it is important to consider that global modulators  
1881 such as tonic arousal are known to have non-linear effects on task performance<sup>65</sup>: In  
1882 perceptual tasks, performance seems to be highest during mid-level arousal, whereas low-  
1883 and high-level arousal lead to reduced accuracy and slower responses<sup>65</sup>. This contrasts  
1884 with the effects of bimodal inference, where accuracy increases linearly as one moves  
1885 from internal to external mode, and responses become faster at both ends of the mode  
1886 spectrum.

1887 • Of note, high phasic arousal has been shown to suppress multi-domain biases in decision-  
1888 making in humans and mice<sup>66-68</sup>, including the biases toward perceptual history<sup>28</sup> that

1889 we implicate in internal mode processing. The increase in response speed and history  
1890 congruence over time (Supplemental Section 9.4) may argue against insufficient training  
1891 as an alternative explanation for internal mode processing, but may also taken as a  
1892 sign of waning arousal. The multiple mechanistic mappings to RTs and confidence  
1893 therefore warrant more direct measures of arousal (such as pupil size<sup>28,65,66,68–70</sup>, motor  
1894 behavior<sup>69,70</sup>, or neural data<sup>71</sup>) to better delineate bimodal inference from fluctuations  
1895 in global modulators of task performance.

1896 **10.1.4 Comment 4**

1897 **In the predictive processing literature, attention is thought to correspond to**  
1898 **fluctuations in sensory and prior precision. Why did you then consider attention**  
1899 **as some additional or unrelated confound?**

1900 This point is closely related to the comment above. We realize that, in the predictive  
1901 processing field, attention is equated with the precision of probability distributions that  
1902 contribute to the perceptual decision, such that an observer can attend strongly to sensory  
1903 information (high likelihood precision) or to internal predictions derived from the sequence of  
1904 preceding percepts (high prior precision). Therefore, when following the above predictive  
1905 processing definition, fluctuations in attention can be equated with fluctuations in mode.

1906 However, we feel that outside of the predictive processing field, attention is not always  
1907 conceived in that way, such that low attention is often considered as low engagement with  
1908 the task, i.e., relating to low likelihood and low prior precision in the predictive processing  
1909 sense. It is against these caveats that our control analysis (based on psychometric functions,  
1910 training effects, RTs and confidence) defend our conclusions on bimodal inference.

1911 We now provide a more nuanced interpretation of our findings of RTs and confidence in  
1912 relation to attention, with a specific focus on predictive processing and precision. We hope  
1913 that our responses to the comment above resolve the points raised in this comment.

<sup>1914</sup> **10.1.5 Comment 5**

<sup>1915</sup> **What licences the assumption that “agents depend upon internal confidence**  
<sup>1916</sup> **signals” in the absence of feedback?**

<sup>1917</sup> In the absence of feedback, observers can only rely on internal estimates of performance to  
<sup>1918</sup> guide updates to their model of the reliability of their sensory apparatus (inferences about  
<sup>1919</sup>  $M$ ). Previous work (e.g. Guggenmos et al., Elife 2106, <https://doi.org/10.7554/eLife.13388>)  
<sup>1920</sup> has shown that confidence signals can provide signals that drive perceptual learning in the  
<sup>1921</sup> absence of feedback. This has motivated our model simulation on the adaptive benefits of  
<sup>1922</sup> bimodal inference for metacognition, where the learning signal  $\epsilon_M$  (i.e., the difference between  
<sup>1923</sup> the choice and its probability) drives inferences about  $M$ . Please note that we have removed  
<sup>1924</sup> this section following Comment 9 of Reviewer 1.

<sup>1925</sup> **10.1.6 Comment 6**

<sup>1926</sup> **And what licences the assumption that internal confidence feedback corresponds**  
<sup>1927</sup> **to “the absolute of the posterior log ratio” (did you mean the log of the posterior**  
<sup>1928</sup> **ratio)?**

<sup>1929</sup> We mean the absolute of the log of the posterior ratio. Following first order models (see  
<sup>1930</sup> e.g., Fleming & Daw, Self-evaluation of decision-making: A general Bayesian framework for  
<sup>1931</sup> metacognitive computation, Psychol. Rev. 2017, <https://doi.org/10.1037/rev0000045>), the  
<sup>1932</sup> perceptual decision and the confidence report rely on the posterior. The distance of the log  
<sup>1933</sup> of the posterior ratio  $L_t$  from zero becomes a measure of decision-certainty or confidence.

<sup>1934</sup> **10.1.7 Comment 7**

<sup>1935</sup> **I got a bit lost here when you say that “the precision of sensory coding M a**  
<sup>1936</sup> **function of u\_t. This is largely because I couldn’t find a definition of u\_t.**

<sup>1937</sup> We apologize for this lack of clarity. In the model simulations on the adaptive benefits of

<sup>1938</sup> bimodal inference, we generated stimuli  $s_t$  from a Bernoulli-distribution with  $p = q = 0.5$ .  
<sup>1939</sup> The value of  $u_t$  was then defined via equation (13), following our modeling of the human  
<sup>1940</sup> data. Please note that we have removed this section following Comment 9 of Reviewer 1.

<sup>1941</sup> **10.1.8 Comment 8**

<sup>1942</sup> **What licences an application of Rescorla-Wagner to learning the parameters (as**  
<sup>1943</sup> **in Equation 11) and, learning sensory precision as described by M\_T (Equation**  
<sup>1944</sup> **13). Are you moving from a Bayesian framework to a reinforcement learning**  
<sup>1945</sup> **framework?**

<sup>1946</sup> We would like to thank the reviewer for pointing out this inconsistency. We have chosen the  
<sup>1947</sup> Rescorla-Wagner learning rule for simplicity: In our model, the speed of learning about  $H$   
<sup>1948</sup> and  $M$  varied according to the current mode of perceptual processing and a constant learning  
<sup>1949</sup> rate. Allowing the learning rate itself to vary as a function of preceding experiences would  
<sup>1950</sup> add an additional level of complexity that we sought to omit in this analysis. However, we  
<sup>1951</sup> fully agree that choosing a Bayesian framework (e.g., a three-level HGF) would indeed be  
<sup>1952</sup> more consistent. Please note that we have removed this section following Comment 9 of  
<sup>1953</sup> Reviewer 1.

<sup>1954</sup> **10.1.9 Comment 9**

<sup>1955</sup> **I am sure you have answers to these questions - but with each new question**  
<sup>1956</sup> **the reader is left more and more skeptical that there is a coherent story behind**  
<sup>1957</sup> **your analyses. It would have been more convincing had you just committed to**  
<sup>1958</sup> **a Bayesian filter and made your points using one update scheme, under ideal**  
<sup>1959</sup> **Bayesian observer assumptions.**

<sup>1960</sup> **Unlike your piecemeal scheme, things like the hierarchical Gaussian filter estimates**  
<sup>1961</sup> **the sensory and prior decisions explicitly and these estimates underwrite posterior**  
<sup>1962</sup> **inference. In your scheme, the sensory precision M appears to have no influence**

1963 on perceptual inference (which is why, presumably you call it metacognition).

1964 The problem with this is that your motivation for systematic fluctuations in

1965 precision is weakened. This is because improved metacognition does not improve

1966 perception — it only improves the perception of perception.

1967 In light of the above, can I suggest that you remove Section 5.8 and use your

1968 model in the preceding section to endorse your hypothesis along the following

1969 lines:

1970 “In summary, we hypothesized that subjects have certain hyperpriors that are

1971 apt for accommodating fluctuations in the predictability of their environment;

1972 i.e., people believe that their world is inherently volatile. This means that to be

1973 Bayes optimal it is necessary to periodically re-evaluate posterior beliefs about

1974 model parameters. One way to do this is to periodically suspend the precision

1975 of prior beliefs and increase the precision afforded to sensory evidence that

1976 updates (Bayesian) beliefs about model parameters. The empirical evidence above

1977 suggests that the timescale of this periodic scheduling of evidence accumulation

1978 may be scale-invariant. This means that there may exist a timescale of periodic

1979 fluctuations in precision over every window or length of perceptual decision-

1980 making. In what follows, we model perceptual decisions under a generative model

1981 (based upon a hazard function to model historical or serial dependencies) with, a

1982 periodic fluctuation in the precision of sensory evidence relative to prior beliefs

1983 at a particular timescale. Remarkably—using Bayesian model comparison—we

1984 find that a model with fluctuating precisions has much greater evidence, relative

1985 to a model in the absence of fluctuating precisions. Furthermore, we were able

1986 to quantify the dominant timescale of periodic fluctuations; appropriate for these

1987 kinds of paradigm.”

1988 Note, again, I am reading your `omega_llr` and `omega_psi` as precisions and

1989 that the periodic modulation is the hyperprior that you are characterizing—and  
1990 have discovered.

1991 We would like to thank Prof. Friston for these very helpful and precise suggestions. In brief,  
1992 we now provide a quantitative assessment of model space based on AIC (i) and have followed  
1993 the suggestion of omitting section 5.8 (ii).

1994 In addition to the qualitative assessment of our models in the initial version of our manuscript,  
1995 we have conducted a formal model comparison (i). Following the model comparisons in  
1996 other sections of the manuscript, we based the model comparison on AIC. We furthermore  
1997 show that the winning *bimodal inference model* predicts out-of-training variables (RT and  
1998 confidence) and use simulations from posterior model parameters to show that, in contrast to  
1999 reduced models, the bimodal inference model neither over- nor underfits the empirical data.

2000 We have added a description of our model comparison to the Method section:

2001 • We validated the bimodal inference model in three steps: a formal model comparison to  
2002 reduced models based on AIC (Figure 1F-G; Supplemental Figure S9), the prediction of  
2003 within-training (stimulus- and history-congruence) as well as out-of-training variables  
2004 (RT and confidence), and a qualitative reproduction of the empirical data from model  
2005 simulations based on estimated parameters (Figure 4).

2006 • **Model comparison.** We assessed the following model space based on AIC:

2007 • The full *bimodal inference model* (M1; Figure 1F) incorporates the influence of sensory  
2008 information according to the parameter  $\alpha$  (likelihood); the integration of evidence across  
2009 trials according to the parameter  $H$  (prior); anti-phase oscillations in between likelihood  
2010 and prior precision according to  $\omega_{LLR}$  and  $\omega_\psi$  with parameters  $a_{LLR}$  (amplitude likelihood  
2011 fluctuation),  $a_\psi$  (amplitude prior fluctuation),  $f$  (frequency) and  $p$  (phase).

2012 • The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the influence of sen-  
2013 sory information according to parameter  $\alpha$  (likelihood); the integration of evidence across

2014 trials according to parameter  $H$  (prior); oscillations in likelihood precision according  
2015 to  $\omega_{LLR}$  with parameters  $a_{LLR}$  (amplitude likelihood fluctuation),  $f$  (frequency) and  $p$   
2016 (phase).

- 2017 • The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory  
2018 information according to parameter  $\alpha$  (likelihood); the integration of evidence across  
2019 trials according to parameter  $H$  (prior); oscillations in the prior precision according  
2020 to  $\omega_\psi$  with parameters  $a_\psi$  (amplitude prior fluctuation),  $f$  (frequency) and  $p$  (phase).  
2021 Please note that all models M1-3 lead to shifts in the relative precision of likelihood and  
2022 prior.

- 2023 • The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the influence of  
2024 sensory information according to parameter  $\alpha$  (likelihood); the integration of evidence  
2025 across trials according to parameter  $H$  (prior), There are no additional oscillations.  
2026 Model M4 thus corresponds to the model proposed by Glaze et al. and captures normative  
2027 evidence accumulation in unpredictable environments using a Bayesian update scheme<sup>51</sup>.  
2028 The comparison against M4 tests the null hypothesis that fluctuations in mode emerge  
2029 from a normative Bayesian model without the ad-hoc addition of oscillations as in models  
2030 M1-3.

- 2031 • The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence of sensory  
2032 information according to parameter  $\alpha$  (likelihood). The model lacks integration of  
2033 evidence across trials (flat prior) and oscillations. The comparison against M5 tests  
2034 the null hypothesis that observers do not use prior information derived from serial  
2035 dependency in perception.

- 2036 • **Prediction of within-training and out-of-training variables.** To validate our  
2037 model, we correlated individual posterior parameter estimates with the respective  
2038 conventional variables. As a sanity check, we tested (i), whether the estimated hazard  
2039 rate  $H$  correlated negatively with the frequency of history-congruent choices and, (ii),

2040 whether the estimated sensitivity to sensory information  $\alpha$  correlated positively with the  
2041 frequency of stimulus-congruent choices. In addition, we tested whether the posterior  
2042 decision certainty (i.e., the absolute of the log posterior ratio) correlated negatively with  
2043 RTs and positively with confidence. This allowed us to assess whether our model could  
2044 explain aspects of the data it was not fitted to (i.e., RTs and confidence).

- 2045 • **Simulations.** Finally, we used simulations (Figure 4, Supplemental Figures S10-13)  
2046 to show that all model components, including the anti-phase oscillations governed by  
2047  $a_\psi$ ,  $a_{LLR}$ ,  $f$  and  $p$ , were necessary for our model to reproduce the characteristics of the  
2048 empirical data. This enabled us to assess over- or under-fitting in the bimodal inference  
2049 model and all reduced models M2-M5. We used the posterior model parameters observed  
2050 for humans ( $H$ ,  $\alpha$ ,  $a_\psi$ ,  $a_{LLR}$ ,  $f$ ,  $p$  and  $\zeta$ ) to define individual parameters for simulation  
2051 in 4317 simulated participants (i.e., equivalent to the number of human participants).  
2052 For each participant, the number of simulated trials was drawn at random between  
2053 300 to 700. Inputs  $s$  were drawn at random for each trial, such that the sequence of  
2054 inputs to the simulation did not contain any systematic seriality. Noisy observations  
2055  $u$  were generated by applying the posterior parameter  $\alpha$  to inputs  $s$ , thus generating  
2056 stimulus-congruent choices in  $71.36 \pm 2.6 \times 10^{-3}\%$  of trials. Choices were simulated  
2057 based on the trial-wise choice probabilities  $y_p$  obtained from our model. Simulated data  
2058 were analyzed in analogy to the human and mouse data. As a substitute of subjective  
2059 confidence, we computed the absolute of the trial-wise log posterior ratio  $|L|$  (i.e., the  
2060 posterior decision certainty).

2061 We have also added a graphical depiction of the model space to Figure 1 (subpanels F and  
2062 G):

- 2063 • F. The bimodal inference model (M1) explains fluctuations between externally- and  
2064 externally-biased modes (left panel) by two interacting factors: a normative accumulation

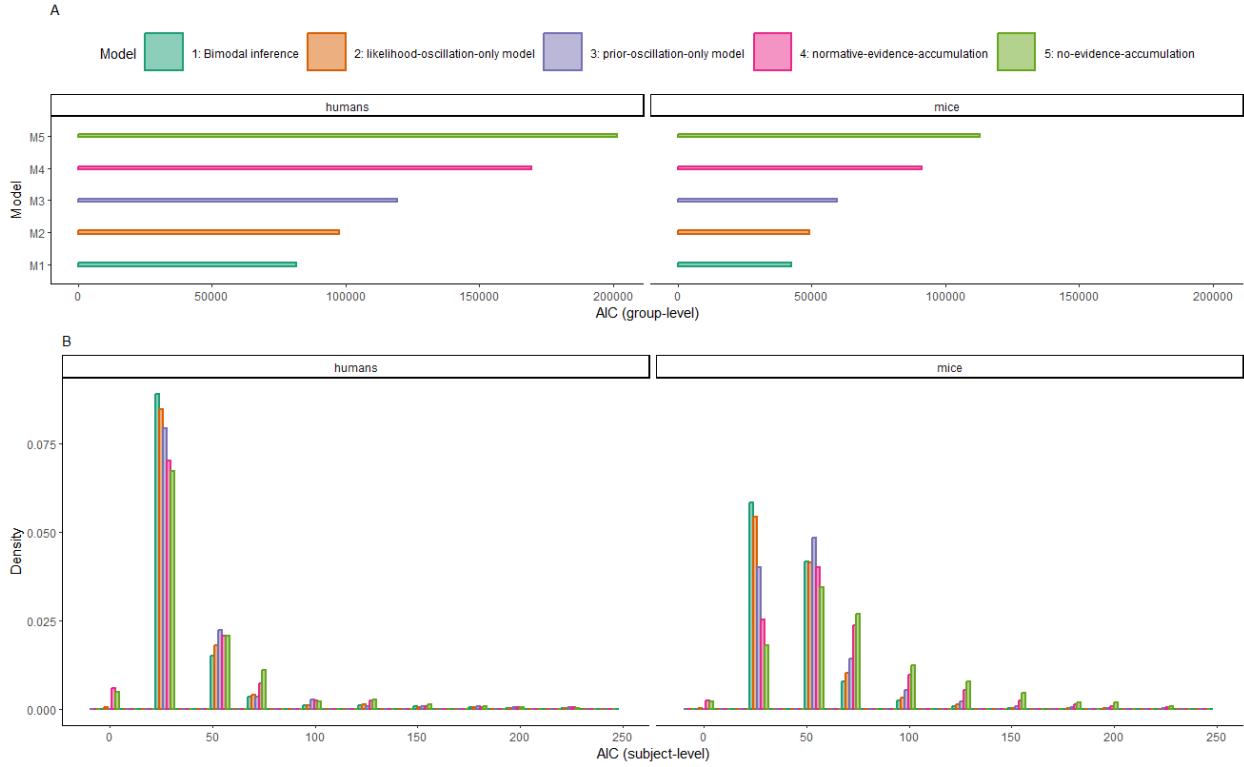


Figure 1 F-G

2065 of evidence according to parameters  $H$  (middle panel), and anti-phase oscillations in the  
 2066 precision terms  $\omega_{LLR}$  and  $\omega_\psi$  (right panel).

- 2067 • G. The control models M2-M5 were constructed by successively removing the anti-phase  
 2068 oscillations and the integration of information from the bimodal inference model. Please  
 2069 note that the normative-evidence-accumulation-model (M4) corresponds to the model  
 2070 proposed by Glaze et al.<sup>51</sup>. In the no-evidence-accumulation model (M5), perceptual  
 2071 decisions depend only on likelihood information (flat priors).

2072 The formal model comparison yielded clear evidence for a superiority of the bimodal inference  
 2073 model, in particular over the normative Bayesian model of evidence accumulation. The model  
 2074 successfully predicted both within-training variables (as a sanity-check) and out-of-training  
 2075 variables. Simulations from posterior model parameters closely followed the empirical data  
 2076 (Figure 4), which was not the case for reduced models (Supplemental Figures S10-13). We

2077 summarize these findings in the Results section and have added a Supplemental Figure S9 to  
2078 show the distribution of observer-level AIC at the session-level (see below):

- 2079 • We used a maximum likelihood procedure to fit the bimodal inference model (M1, Figure  
2080 1F) to the behavioral data from the Confidence database<sup>20</sup> and the IBL database<sup>21</sup>,  
2081 optimizing the parameters  $\alpha$ ,  $H$ ,  $amp_{LLR}$ ,  $amp_\psi$ ,  $f$ ,  $p$ , and  $\zeta$  (see Methods for details and  
2082 Supplemental Table T2 for a summary of the parameters of the bimodal inference model).  
2083 We validated our model in three steps: First, to show that bimodal inference does not  
2084 emerge spontaneously in normative Bayesian models of evidence accumulation, but  
2085 requires the ad-hoc addition of anti-phase oscillations in prior and likelihood precision,  
2086 we compared the bimodal inference model to four control models (M2-5, Figure 1G).  
2087 In these models, we successively removed the anti-phase oscillations (M2-M4) and the  
2088 integration of information across trials (M5) from the bimodal inference model and  
2089 performed a model comparison based on AIC.
- 2090 • Model M2 ( $AIC_2 = 9.76 \times 10^4$  in humans and  $4.91 \times 10^4$  in mice) and Model M3 ( $AIC_3$   
2091  $= 1.19 \times 10^5$  in humans and  $5.95 \times 10^4$  in mice) incorporated only oscillations of either  
2092 likelihood or prior precision. Model M4 ( $AIC_4 = 1.69 \times 10^5$  in humans and  $9.12 \times 10^4$  in  
2093 mice) lacked any oscillations of likelihood and prior precision and corresponded to the  
2094 normative model proposed by Glaze et al.<sup>51</sup>. In model M5 ( $AIC_4 = 2.01 \times 10^5$  in humans  
2095 and  $1.13 \times 10^5$  in mice), we furthermore removed the integration of information across  
2096 trials, such that perception depended only in incoming sensory information (Figure 1G).
- 2097 • The bimodal inference model achieved the lowest AIC across the full model space ( $AIC_1$   
2098  $= 8.16 \times 10^4$  in humans and  $4.24 \times 10^4$  in mice) and was clearly superior to the normative  
2099 Bayesian model of evidence accumulation ( $\delta_{AIC} = -8.79 \times 10^4$  in humans and  $-4.87 \times 10^4$   
2100 in mice; Supplemental Figure S9).
- 2101 • As a second validation of the bimodal inference model, we tested whether the posterior  
2102 model predicted within-training and out-of-training variables. The bimodal inference

model characterizes each subject by a sensitivity parameter  $\alpha$  (humans:  $\alpha = 0.5 \pm 1.12 \times 10^{-4}$ ; mice:  $\alpha = 1.06 \pm 2.88 \times 10^{-3}$ ) that captures how strongly perception is driven by the available sensory information, and a hazard rate parameter  $H$  (humans:  $H = 0.45 \pm 4.8 \times 10^{-5}$ ; mice:  $H = 0.46 \pm 2.97 \times 10^{-4}$ ) that controls how heavily perception is biased by perceptual history. The parameter  $f$  captures the dominant time scale at which likelihood (amplitude humans:  $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$ ; mice:  $a_{LLR} = 0.39 \pm 1.08 \times 10^{-3}$ ) and prior precision (amplitude humans:  $a_\psi = 1.44 \pm 5.27 \times 10^{-4}$ ; mice:  $a_\psi = 1.71 \pm 7.15 \times 10^{-3}$ ) fluctuated and was estimated at  $0.11 \pm 1.68 \times 10^{-5} 1/N_{trials}$  and  $0.11 \pm 1.63 \times 10^{-4} 1/N_{trials}$  in mice.

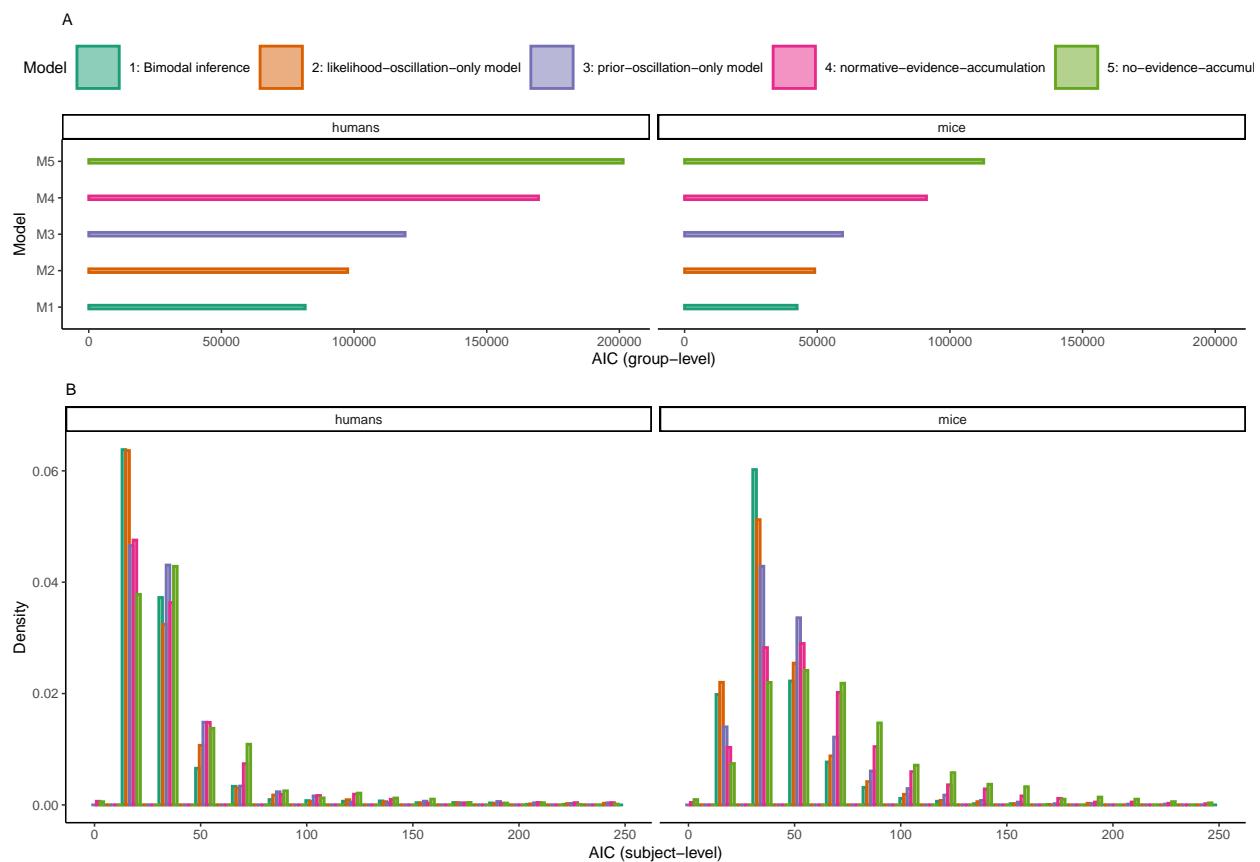
- As a sanity check for model fit, we tested whether the frequency of stimulus- and history-congruent trials in the Confidence database<sup>20</sup> and IBL database<sup>21</sup> correlate with the estimated parameters  $\alpha$  and  $H$ , respectively. As expected, the estimated sensitivity toward stimulus information  $\alpha$  was positively correlated with the frequency of stimulus-congruent perceptual choices (humans:  $\beta = 8.4 \pm 0.26$ ,  $T(4.31 \times 10^3) = 32.87$ ,  $p = 1.3 \times 10^{-211}$ ; mice:  $\beta = 1.93 \pm 0.12$ ,  $T(2.07 \times 10^3) = 16.21$ ,  $p = 9.37 \times 10^{-56}$ ). Likewise,  $H$  was negatively correlated with the frequency of history-congruent perceptual choices (humans:  $\beta = -11.84 \pm 0.5$ ,  $T(4.29 \times 10^3) = -23.5$ ,  $p = 5.16 \times 10^{-115}$ ; mice:  $\beta = -6.18 \pm 0.66$ ,  $T(2.08 \times 10^3) = -9.37$ ,  $p = 1.85 \times 10^{-20}$ ).
- Our behavioral analyses reveal that humans and mice show significant effects of perceptual history that impaired performance in randomized psychophysical experiments<sup>24,28,30,31,43</sup> (Figure 2A and 3A). We therefore expected that humans and mice underestimated the true hazard rate  $\hat{H}$  of the experimental environments (Confidence database<sup>20</sup>:  $\hat{H}_{Humans} = 0.5 \pm 1.58 \times 10^{-5}$ ); IBL database<sup>21</sup>:  $\hat{H}_{Mice} = 0.49 \pm 6.47 \times 10^{-5}$ ). Indeed, when fitting the bimodal inference model to the trial-wise perceptual choices, we found that the estimated (i.e., subjective) hazard rate  $H$  was lower than  $\hat{H}$  for both humans ( $\beta = -6.87 \pm 0.94$ ,  $T(61.87) = -7.33$ ,  $p = 5.76 \times 10^{-10}$ ) and mice ( $\beta = -2.91 \pm 0.34$ ,

2129  $T(112.57) = -8.51$ ,  $p = 8.65 \times 10^{-14}$ .

- 2130 • To further probe the validity of the bimodal inference model, we tested whether posterior  
2131 model quantities could explain aspects of the behavioral data that the model was not  
2132 fitted to. We predicted that the posterior decision variable  $L_t$  not only encodes perceptual  
2133 choices (i.e., the variable used for model estimation), but should also predict the speed  
2134 of response and subjective confidence<sup>30,44</sup>. Indeed, the estimated trial-wise posterior  
2135 decision certainty  $|L_t|$  correlated negatively with RTs in humans ( $\beta = -4.36 \times 10^{-3} \pm$   
2136  $4.64 \times 10^{-4}$ ,  $T(1.98 \times 10^6) = -9.41$ ,  $p = 5.19 \times 10^{-21}$ ) and TDs mice ( $\beta = -35.45 \pm$   
2137  $0.86$ ,  $T(1.28 \times 10^6) = -41.13$ ,  $p < 2.2 \times 10^{-308}$ ). Likewise, subjective confidence reports  
2138 were positively correlated with the estimated posterior decision certainty in humans ( $\beta$   
2139  $= 7.63 \times 10^{-3} \pm 8.32 \times 10^{-4}$ ,  $T(2.06 \times 10^6) = 9.18$ ,  $p = 4.48 \times 10^{-20}$ ).
- 2140 • The dynamic accumulation of information inherent to our model entails that biases  
2141 toward perceptual history are stronger when the posterior decision certainty at the  
2142 preceding trial is high<sup>30,31,51</sup>. Due to the link between posterior decision certainty and  
2143 confidence, we reasoned that confident perceptual choices should be more likely to induce  
2144 history-congruent perception at the subsequent trial<sup>30,31</sup>. Indeed, logistic regression  
2145 indicated that history-congruence was predicted by the posterior decision certainty  
2146  $|L_{t-1}|$  (humans:  $\beta = 8.22 \times 10^{-3} \pm 1.94 \times 10^{-3}$ ,  $z = 4.25$ ,  $p = 2.17 \times 10^{-5}$ ; mice:  $\beta =$   
2147  $-3.72 \times 10^{-3} \pm 1.83 \times 10^{-3}$ ,  $z = -2.03$ ,  $p = 0.04$ ) and subjective confidence (humans:  
2148  $\beta = 0.04 \pm 1.62 \times 10^{-3}$ ,  $z = 27.21$ ,  $p = 4.56 \times 10^{-163}$ ) at the preceding trial.
- 2149 • As a third validation of the bimodal inference model, we used the posterior model  
2150 parameters to simulate synthetic perceptual choices and repeated the behavioral analyses  
2151 conducted for the empirical data. Simulations from the bimodal inference model  
2152 closely replicated our empirical results: Simulated perceptual decisions resulted from a  
2153 competition of perceptual history with incoming sensory signals (Figure 4A). Stimulus-  
2154 and history-congruence were significantly autocorrelated (Figure 4B-C), fluctuating in

anti-phase as a scale-invariant process with a 1/f power law (Figure 4D-F). Simulated posterior certainty<sup>28,30,44</sup> (i.e., the absolute of the log posterior ratio  $|L_t|$ ) showed a quadratic relationship to the mode of sensory processing (Figure 4H), mirroring the relation of RTs and confidence reports to external and internal biases in perception (Figure 2G-H and Figure 3G-H). Crucially, the overlap between empirical and simulated data broke down when we removed the anti-phase oscillations or the accumulation of evidence over time from the bimodal inference model (Supplemental Figure S10-13).

- In sum, computational modeling suggested that between-mode fluctuations are best explained by two interlinked processes (Figure 1E): (i), the dynamic accumulation of information across successive trials mandated by normative Bayesians model of evidence accumulation and, (ii), ongoing anti-phase oscillations in the impact of external and internal information.



2168 • **Supplemental Figure S9.** Comparison of the bimodal inference model against reduced  
2169 control models.

- 2170 • A. Group-level AIC. The bimodal inference model (M1) achieved the lowest AIC across  
2171 the full model space ( $AIC_1 = 8.16 \times 10^4$  in humans and  $4.24 \times 10^4$  in mice). Model  
2172 M2 ( $AIC_2 = 9.76 \times 10^4$  in humans and  $4.91 \times 10^4$  in mice) and Model M3 ( $AIC_3 =$   
2173  $1.19 \times 10^5$  in humans and  $5.95 \times 10^4$  in mice) incorporated only oscillations of either  
2174 likelihood or prior precision. Model M4 ( $AIC_4 = 1.69 \times 10^5$  in humans and  $9.12 \times 10^4$   
2175 in mice) lacked any oscillations of likelihood and prior precision and corresponded to  
2176 the normative model proposed by Glaze et al.<sup>51</sup>. In model M5 ( $AIC_5 = 2.01 \times 10^5$  in  
2177 humans and  $1.13 \times 10^5$  in mice), we furthermore removed the integration of information  
2178 across trials, such that perception depended only in incoming sensory information.
- 2179 • B. Subject-level AIC. Here, we show the distribution of AIC values at the subject-level.  
2180 AIC for the bimodal inference model tended to be smaller than AIC for the comparator  
2181 models (statistical comparison to the second-best model M2 in humans:  $\beta = -1.71$   
2182  $\pm 0.19$ ,  $T(8.57 \times 10^3) = -8.85$ ,  $p = 1.06 \times 10^{-18}$ ; mice:  $T(1.57 \times 10^3) = -3.08$ ,  $p =$   
2183  $2.12 \times 10^{-3}$ ).

2184 In light of our response to Comments 1 - 9 of Reviewer 1, we agree that a complete and  
2185 extensive investigation of the relation between bimodal inference, learning about changes in  
2186 the environment and the relation to metacognition may be beyond the scope of the current  
2187 manuscript: Both Reviewer 1 and 3 (see below) have shared that the manuscript is too long  
2188 and should be streamlined. Yet evaluating the full model space (e.g., comparing update rules  
2189 for inferences about  $H$  and  $M$ , testing for an influence of beliefs about  $M$  on learning about  $H$   
2190 etc.) would make the manuscript even longer. We are therefore happy to follow Prof. Fristons  
2191 suggestions to omit section 5.8. We have changed the manuscript in the following ways:

2192 When introducing  $\omega_{LLR}$ , we identify it as the precision afforded to the likelihood, referring to  
2193 the Bayesian framework, and refer to fluctuations in mode as a hyperprior.

2194 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-  
2195 biased modes of perceptual processing that occur irrespective of the sequence of preceding  
2196 experiences, we assumed that likelihood and prior vary in their influence on the perceptual  
2197 decision according to fluctuations governed by  $\omega_{LLR}$  and  $\omega_\psi$ . These anti-phase sine  
2198 functions (defined by amplitudes  $a_{LLR/\psi}$ , frequency  $f$  and phase  $p$ ) determine the  
2199 precision afforded to the likelihood and prior<sup>53</sup>. The implicit anti-phase fluctuations  
2200 are mandated by Bayes-optimal formulations in which inference depends only on the  
2201 relative values of prior and likelihood precision (i.e., the Kalman gain<sup>54</sup>). As such,  $\omega_{LLR}$   
2202 and  $\omega_\psi$  implement a hyperprior<sup>55</sup> in which the likelihood and prior precisions are shifted  
2203 against each other at a dominant timescale defined by  $f$ .

2204 We have deleted the section 5.8 and added a summary of our modeling approach to the  
2205 discussion, closely following the text recommended by Prof. Friston:

2206 • (...) Yet relying too strongly on serial dependencies may come at a cost: When  
2207 accumulating over time, internal predictions may eventually override external information,  
2208 leading to circular and false inferences about the state of the environment<sup>57</sup>. Akin to the  
2209 wake-sleep-algorithm in machine learning<sup>58</sup>, bimodal inference may help to determine  
2210 whether errors result from external input or from internally-stored predictions: During  
2211 internal mode, sensory processing is more strongly constrained by predictive processes  
2212 that auto-encode the agent's environment. Conversely, during external mode, the  
2213 network is driven predominantly by sensory inputs<sup>18</sup>. Between-mode fluctuations may  
2214 thus generate an unambiguous error signal that aligns internal predictions with the  
2215 current state of the environment in iterative test-update-cycles<sup>58</sup>. On a broader scale,  
2216 between-mode fluctuations may thus regulate the balance between feedforward versus  
2217 feedback contributions to perception and thereby play a adaptive role in metacognition  
2218 and reality monitoring<sup>59</sup>.

2219 • We hypothesized that observers have certain hyperpriors that are apt for accommodating

fluctuations in the predictability of their environment, i.e., people believe that their world is inherently volatile. To be Bayes optimal, it is therefore necessary to periodically re-evaluate posterior beliefs about the parameters that define an internal generative model of the external sensory environment. One way to do this is to periodically suspend the precision of prior beliefs and increase the precision afforded to sensory evidence, thus updating Bayesian beliefs about model parameters.

- The empirical evidence above suggests that the timescale of this periodic scheduling of evidence accumulation may be scale-invariant. This means that there may exist a timescale of periodic fluctuations in precision over every window or length of perceptual decision-making. Bimodal inference predicts perceptual decisions under a generative model (based upon a hazard function to model serial dependencies between subsequent trials) with periodic fluctuations in the precision of sensory evidence relative to prior beliefs at a particular timescale. Remarkably, a systematic model comparison based on AIC indicated that a model with fluctuating precisions has much greater evidence, relative to a model in the absence of fluctuating precisions. This ad-hoc addition of oscillations to a normative Bayesian model of evidence accumulation<sup>51</sup> allowed us to quantify the dominant timescale of periodic fluctuations mode at approximately 0.11  $1/N_{trials}$  in humans and mice that is appropriate for these kinds of paradigms.

Following the deletion of section 5.8, we have adapted the last sentence of the abstract and the last paragraph of the introduction:

- (...) We propose that between-mode fluctuations generate unambiguous error signals that enable optimal inference in volatile environments.
- When less sensitive to external stimulus information, humans and mice did not behave more randomly, but showed stronger serial dependencies in their perceptual choices<sup>22–33</sup>. These serial dependencies may be understood as driven by internal predictions that reflect

2245 the autocorrelation of natural environments<sup>34</sup> and bias perception toward preceding  
2246 experiences<sup>30,31,35</sup>. Computational modeling indicated that ongoing changes in perceptual  
2247 performance may be driven by systematic fluctuations between externally- and internally-  
2248 oriented modes of sensory analysis. We suggest that such *bimodal inference* may help  
2249 to build stable internal representations of the sensory environment despite an ongoing  
2250 stream of sensory information.

#### 2251 10.1.10 Comment 11

2252 This begs the question as to whether you want to pursue the 1/f story. You  
2253 refer to this as “noise”. However, there is no noise in this setup. I think what  
2254 you meant was that the fluctuations are scale free, because they evinced a power  
2255 law. I am sure that there are scale free aspects of these kinds of hyperpriors;  
2256 however, in the context of your paradigm I wonder whether you should just  
2257 ignore the scale free aspect and focus on your estimated temporal scale implicit  
2258 in  $f$ . This means you don’t have to hand wave about self-organized criticality in  
2259 the discussion and focus upon your hypothesis.

2260 We would like to thank the reviewer for this suggestion. We agree that the discussion  
2261 of self-organized criticality is far from the data. We have omitted this section from the  
2262 discussion. With respect to  $f$ , we have adapted the manuscript to make clear that it captures  
2263 the dominant timescale of fluctuations in mode:

- 2264 • (...) This implements a hyperprior<sup>55</sup> in which the likelihood and prior precisions are  
2265 shifted against each other at a dominant timescale defined by  $f$ : (...)
- 2266 • (...) The parameter  $f$  captured the dominant time scale at which likelihood and prior  
2267 precision were shifted against each other and was estimated at 0.11  $1/N_{trials}$  in both  
2268 humans and mice.

2269 • Remarkably, a systematic model comparison based on AIC indicated that a model with  
2270 fluctuating precisions has much greater evidence, relative to a model in the absence  
2271 of fluctuating precisions. The ad-hoc addition of oscillations to a normative Bayesian  
2272 model of evidence accumulation<sup>51</sup> allowed us to quantify the dominant timescale of  
2273 periodic fluctuations mode at approximately  $0.11 \text{ } 1/N_{trials}$  in humans and mice that is  
2274 appropriate for these kinds of paradigms.

2275 **10.1.11 Comment 12**

2276 **A final move—to make the paper more focused and digestible—would be to**  
2277 **put a lot of your defensive analyses (e.g. about general arousal et cetera) in**  
2278 **supplementary material. You have to be careful not to exhaust the reader by**  
2279 **putting up a lot of auxiliary material before the important messages in your**  
2280 **report.**

2281 We have followed this suggestion and move the following sections to the Supplement: section  
2282 5.3 (Internal and external modes of processing facilitate response behavior and enhance  
2283 confidence in human perceptual decision-making), section 5.4 (Fluctuations between internal  
2284 and external mode modulate perceptual performance beyond the effect of general response  
2285 biases), section 5.5 (Internal mode is characterized by lower thresholds as well as by history-  
2286 dependent changes in biases and lapses). We have also moved secondary statistics to the  
2287 figure legends and to the Supplement.

2288 **Minor points**

2289 **10.1.12 Comment 13**

2290 **I cannot resist suggesting that you change your title to “Bimodal Inference in**  
2291 **Mice and Men”**

2292 We would like to thank the Reviewer for this suggestion and agree that this would indeed  
2293 sound great. However, we are worried that changing the title to *mice and men* would not

2294 be as gender-neutral as *humans and mice*. We would therefore propose to stay with the  
2295 current title. If we are mistaken and *mice and men* can be considered gender-neutral (we are  
2296 non-native speakers), we would be happy to change the title.

2297 **10.1.13 Comment 14**

2298 Please replace “infra-slow fluctuations” with “slow fluctuations”. Slow has some  
2299 colloquial meaning in fMRI studies but not in any scale free context.

2300 Done.

2301 **10.1.14 Comment 15**

2302 Please replace “simulated data” with “simulations” in the abstract. Finally,  
2303 please replace “robust learning and metacognition in volatile environments” with  
2304 “enable optimal inference and learning in volatile environments.”

2305 Done. Since we have followed the suggestion to delete section 5.8, we have rephrased the last  
2306 paragraph of the abstract into:

2307 • (...) We propose that between-mode fluctuations generate unambiguous error signals  
2308 that enable optimal inference in volatile environments.

2309 **10.1.15 Comment 16**

2310 Line 50, please replace “about the degree of noise inherent in encoding of  
2311 sensory information” with “the precision of sensory information relative to prior  
2312 (Bayesian) beliefs.”

2313 Done.

2314 **10.1.16 Comment 17**

2315 Line 125: please replace “a source of error” with “a source of bias”

<sub>2316</sub> Done.

<sub>2317</sub> **10.1.17 Comment 18**

<sub>2318</sub> **Line 141:** please replace “one 1/f noise” with a scale-invariant process with a 1/f  
<sub>2319</sub> power law” (here and throughout) this is not “noise” it is a particular kind of  
<sub>2320</sub> fluctuation.

<sub>2321</sub> Done.

<sub>2322</sub> **10.1.18 Comment 19**

<sub>2323</sub> Line 178, when you say that the fluctuations may arise due to “changes in level of  
<sub>2324</sub> tonic arousal or on-task attention”, I think you need to qualify this. In predictive  
<sub>2325</sub> processing, on-task attention is exactly the modulation of sensory precision,  
<sub>2326</sub> relative to prior precision that you are characterizing here. Tonic arousal may be  
<sub>2327</sub> another thing may or may not confound your current results.

<sub>2328</sub> Thank you very much for pointing this out. We have adapted the discussion to make the  
<sub>2329</sub> distinction between attention in the predictive processing sense and the broader issue of task  
<sub>2330</sub> engagement (reflecting fluctuations in arousal, fatigue etc.) clearer (see also our responses  
<sub>2331</sub> above):

- <sub>2332</sub> • As a functional explanation for bimodal inference, we propose that perception temporarily  
<sub>2333</sub> disengages from internal predictions to form stable inferences about the statistical  
<sub>2334</sub> properties of the sensory environment. Between-mode fluctuations may thus elude  
<sub>2335</sub> circular inferences that occur when both the causes and the encoding of sensory stimuli  
<sub>2336</sub> are volatile<sup>19,57</sup>). By the same token, we suggest that fluctuations in mode occur at  
<sub>2337</sub> the level of perceptual processing<sup>26,30,46,47</sup>, and are not a passive phenomenon that is  
<sub>2338</sub> primarily driven by factors situated up- or downstream of sensory analysis.

- 2339 • How does attention relate to between-mode fluctuations? According to predictive  
2340 processing, attention corresponds to the precision afforded to the probability distributions  
2341 that underlie perceptual inference<sup>53</sup>. As outlined above, between-mode fluctuations  
2342 can be understood as ongoing shifts in the precision afforded to likelihood (*external*  
2343 *mode*) and prior (*internal mode*), respectively. When the precision afforded to prior or  
2344 likelihood increases, posterior precision increases, which leads to faster RTs and higher  
2345 confidence. When defined from the perspective of predictive processing as the precision  
2346 afforded to likelihood and prior<sup>53</sup>, fluctuations in attention may thus provide a plausible  
2347 explanation for the quadratic relationship between mode and RTs and confidence (Figure  
2348 2H and J; Figure 3I; Figure 3I).
- 2349 • Outside of the predictive processing field, attention is often understood in the context of  
2350 task engagement<sup>63</sup>, which varies according to the availability of cognitive resources that  
2351 are modulated by factors such as tonic arousal, familiarity with the task, or fatigue<sup>63</sup>. Our  
2352 results suggest that internal mode processing cannot be completely reduced to intervals  
2353 of low task engagement: In addition to shorter RTs and elevated confidence, choices  
2354 during internal mode were not random or globally biased, but driven by perceptual  
2355 history (Supplemental Figures S6-7). Moreover, our computational model identified  
2356 the dominant timescale of between-mode fluctuations at  $0.11 \sqrt{N_{trials}}$ , which may be  
2357 compatible with fluctuations in arousal<sup>64</sup>, but is faster than to be expected for the  
2358 development of task familiarity or fatigue.
- 2359 • However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,  
2360 speed of response and confidence, it is important to consider that global modulators  
2361 such as tonic arousal are known to have non-linear effects on task performance<sup>65</sup>: In  
2362 perceptual tasks, performance seems to be highest during mid-level arousal, whereas low-  
2363 and high-level arousal lead to reduced accuracy and slower responses<sup>65</sup>. This contrasts  
2364 with the effects of bimodal inference, where accuracy increases linearly as one moves

2365 from internal to external mode, and responses become faster at both ends of the mode  
2366 spectrum.

- 2367 • Of note, high phasic arousal has been shown to suppress multi-domain biases in decision-  
2368 making in humans and mice<sup>66–68</sup>, including the biases toward perceptual history<sup>28</sup> that  
2369 we implicate in internal mode processing. The increase in response speed and history  
2370 congruence over time (Supplemental Section 9.4) may argue against insufficient training  
2371 as an alternative explanation for internal mode processing, but may also taken as a  
2372 sign of waning arousal. The multiple mechanistic mappings to RTs and confidence  
2373 therefore warrant more direct measures of arousal (such as pupil size<sup>28,65,66,68–70</sup>, motor  
2374 behavior<sup>69,70</sup>, or neural data<sup>71</sup>) to better delineate bimodal inference from fluctuations  
2375 in global modulators of task performance.

2376 **10.1.19 Comment 20**

2377 **When introducing Equation 2, please make it clear that the omega terms stand in**  
2378 **for the precisions afforded to the likelihood (omega\_LLl) and prior (omega\_psi)**  
2379 **that constitute the log posterior.**

2380 We have modified the introduction of equation 2 as follows:

- 2381 • Following Bayes' theorem, we reasoned that binary perceptual decisions depend on the  
2382 log posterior ratio  $L$  of the two alternative states of the environment that participants  
2383 learn about via noisy sensory information<sup>51</sup>. We computed the posterior by combining  
2384 the sensory evidence available at time-point  $t$  (i.e., the log likelihood ratio  $LLR$ ) with  
2385 the prior probability  $\psi$ , weighted by the respective precision terms  $\omega_{LLR}$  and  $\omega_\psi$ :

2386 **You can then motivate Equation 6 and 7 as implementing the hyperprior in which**  
2387 **the sensory and prior precisions fluctuate at a particular time scale.**

2388 We would like to thank the reviewer for this suggestion, which we have added to the  
2389 introduction of equations (6) and (7):

- 2390 • To allow for *bimodal inference*, i.e., alternating periods of internally- and externally-  
2391 biased modes of perceptual processing that occur irrespective of the sequence of preceding  
2392 experiences, we assumed that likelihood and prior vary in their influence on the perceptual  
2393 decision according to fluctuations governed by  $\omega_{LLR}$  and  $\omega_\psi$ . These anti-phase sine  
2394 functions (defined by amplitudes  $a_{LLR/\psi}$ , frequency  $f$  and phase  $p$ ) determine the  
2395 precision afforded to the likelihood and prior<sup>53</sup>. The implicit anti-phase fluctuations  
2396 are mandated by Bayes-optimal formulations in which inference depends only on the  
2397 relative values of prior and likelihood precision (i.e., the Kalman gain<sup>54</sup>). As such,  $\omega_{LLR}$   
2398 and  $\omega_\psi$  implement a hyperprior<sup>55</sup> in which the likelihood and prior precisions are shifted  
2399 against each other at a dominant timescale defined by  $f$ : (...)

2400 **10.1.20 Comment 21**

2401 You can also point out that the implicit anti-phase fluctuations are mandated by  
2402 Bayes optimal formulations in which it is only the relative values of the prior  
2403 and sensory precision that matter. Bayesian filters these precisions constitute  
2404 the Kalman gain. You can find a derivation of why this in treatments of the  
2405 hierarchical Gaussian filter is by Mathys et al.

2406 We would like to thank the reviewer for this suggestion. We added this information to the  
2407 description of our model in the Results section (see comment above).

2408 **10.1.21 Comment 22**

2409 In your first model simulations, I would make it clear in the main text which  
2410 parameters you are optimizing's; namely (H, alpha, a\_likelihood, a\_prior f).  
2411 Perhaps a little table with a brief description of the meaning of these hyper  
2412 parameters would be useful?

2413 We now identify the optimized parameters at the outset of the modeling section:

2414 • (...) We used a maximum likelihood procedure to fit the bimodal inference model  
2415 (M1, Figure 1F) to the behavioral data from the Confidence database<sup>20</sup> and the IBL  
2416 database<sup>21</sup>, optimizing the parameters  $\alpha$ ,  $H$ ,  $amp_{LLR}$ ,  $amp_\psi$ ,  $f$ ,  $p$ , and  $\zeta$  (see Methods  
2417 for details and Supplemental Table T2 for a summary of the parameters of the bimodal  
2418 inference model). We validated our model in three steps: (...).

2419 We furthermore included a table summarizing the model parameters in the Supplement.

#### 2420 10.1.22 Comment 23

2421 Please remove Section 5.8. If you do not, you need to explain why — on line 586  
2422 - setting  $a = 0$  is appropriate when  $a = 0$ , the log posterior in Equation 2 is zero  
2423 because the precisions (omegas) are zero (by Equations 6 and 7).

2424 We have removed the section 5.8. When setting the amplitude parameters to zero,  $\omega_{LLR}$  and  
2425  $\omega_\psi$  are constant at 1, creating a unimodal control model that corresponds to the normative  
2426 Bayesian evidence accumulation model proposed by Glaze et al<sup>51</sup>.

#### 2427 10.2 Reviewer 2

2428 The authors elucidate whether periodicities in the sensitivity to external informa-  
2429 tion represent an epiphenomenon of limited processing capacity or, alternatively,  
2430 result from a structured and adaptive mechanism of perceptual inference. Ana-  
2431 lyzing large datasets of perceptual decision-making in humans and mice, they  
2432 investigated whether the accuracy of visual perception is constant over time  
2433 or whether it fluctuates. The authors found significant autocorrelations on the  
2434 group level and on the level of individual participants, indicating that a stimulus-  
2435 congruent response in a given trial increased the probability of stimulus-congruent

2436 responses in the future. Furthermore, the authors addressed whether observers  
2437 cycle through periods of enhanced and reduced sensitivity to external information  
2438 or whether observers rely on internal information in certain phases. This was  
2439 quantified by whether a response at a given trial was correlated with responses  
2440 in previous trials. The authors used computational modeling to infer the origin  
2441 of the different modes (internal vs. external).

2442 **Evaluation**

2443 This is a very interesting and well-written manuscript, dealing with an important  
2444 question. The findings are novel and provide an innovative account of interpreting  
2445 visual perception. I am not an expert in modeling, so I will restrict my comments  
2446 to theoretical framework and the experimental approach. I have a few minor  
2447 questions that I would like the authors to answer or clarify.

2448 We would like to thank the reviewer for the evaluation of our manuscript. We have added  
2449 the discussion of potential effects at the motor-level to our discussion.

2450 **Minor questions**

2451 **10.2.1 Comment 1**

2452 History congruent perception was defined on the basis of response repetitions.  
2453 Are we really sure that responses are repeated due to some variant of a per-  
2454 ceptual decision process (internal or external) or may arise on the motor-level -  
2455 independent of a perceptual source? For instance, a response primed by residual  
2456 activation in the motor system may represent a local effect independent from a  
2457 general response bias. If indeed, a response repetition is initiated by whatever  
2458 reasons (non-perceptual), wouldn't this imply that the repeated response is  
2459 per se more related to previous than to current visual information and would  
2460 hence signal a reduced sensitivity to current external information? The authors

2461 are discussing the option of stereotypically repeated responses in the context  
2462 of alertness. However, a tendency to repeat responses may arise due to other  
2463 reasons. For instance, may the motor priming effects mentioned possibly explain  
2464 faster RTs along with a stronger bias when in internal-mode.

2465 Thanks a lot for pointing this out. In this manuscript, we attempt to characterize the  
2466 phenomenon of bimodal inference at the level of behavior: The Confidence database consists  
2467 only of behavioral data. At the time of publishing this paper as a preprint, the IBL database  
2468 had also released only behavioral data.

2469 We realize that it is very difficult to preclude all influences from effects that occur at the  
2470 level of behavior. Not all studies in the confidence database have used a counter-balanced  
2471 mapping between the perceptual decision and the associated motor-response. In the IBL  
2472 data, the mapping between the perceptual decision and the associated motor-response is  
2473 fixed (turning a response wheel left or right depending on the perceived location of a grating).  
2474 Confidence reports also provide only indirect information on motor- vs. perceptual effects.  
2475 One may speculate that, if a response was driven by residual activity in the motor system, it  
2476 may be more likely to be a lapse and be accompanied by reduced confidence. By contrast,  
2477 we found that confidence was, on average, elevated for history-congruent choices.

2478 That being said, behavioral analyses alone are insufficient to rule out the contribution of  
2479 motor-related effects to seriality in choices. This would require analyses of additional types  
2480 of data, such as video tracking of the motor response or even neural data collected in brain  
2481 areas directly related to motor behavior. While this analysis is beyond the scope of the  
2482 present manuscript, we plan to carry out these analyses using the recent data publication of  
2483 the IBL, that contains, among others, video tracking of the motor response (turning of the  
2484 response wheel) and neuropixel recording across the whole brain, including premotor and  
2485 motor cortex<sup>71</sup>.

2486 We have added these considerations to the discussion of potential confounds:

- 2487 • Residual activation of the motor system may provide another contribution to serial biases  
2488 in perceptual choices<sup>72</sup>. Such motor-driven priming may lead to errors in randomized  
2489 psychophysical designs, resembling the phenomenon that we identify as internally-biased  
2490 processing<sup>73</sup>. Moreover, residual activation of the motor system may lead to faster  
2491 responses, and thus constitutes an alternative explanation for the quadratic relationship  
2492 of mode with RTs<sup>72</sup>. The observation of elevated confidence for stronger biases toward  
2493 internal mode speaks against the proposition that residual activation of the motor system  
2494 is the primary driver of serial choice biases, since strong motor-driven priming should lead  
2495 to frequent lapses that are typically associated reduced confidence<sup>74</sup>. Likewise, perceptual  
2496 history effects have repeatedly been replicated in experiments with counter-balanced  
2497 stimulus-response mappings<sup>82</sup>.
- 2498 • No-response paradigms, in which perceptual decision are inferred from eye-  
2499 movements alone, could help to better differentiate perceptual from motor-  
2500 related effects. Likewise, video-tracking of response behavior and neural  
2501 recording from motor- and premotor, which has recently been released for  
2502 the IBL database<sup>71</sup>, may provide further insight into the relation of motor  
2503 behavior to the perceptual phenomenon of between-mode fluctuations.

### 2504 10.3 Reviewer 3

2505 In this paper the authors propose that during perceptual decisions, humans and  
2506 mice exhibit regular oscillatory fluctuations between an “external” (that places  
2507 more weight on the perceptual evidence) and an “internal” (that places more  
2508 weight on historical experiences) mode. In particular, the authors propose a  
2509 computational scheme in which the influences of history and current stimulus on  
2510 choice oscillate in anti phase, effectively implementing “bimodal inference”. The  
2511 computational advantages of these scheme as well as its relation to the underlying  
2512 neurophysiology are discussed.

2513 Overall, the authors make a very interesting proposal about what drives slow  
2514 fluctuations in perceptual performance during randomized two-alternative choice  
2515 tasks. This proposal relates changes in accuracy with changes in serial choice  
2516 biases, which is a timely and synthesizing contribution. Furthermore, this proposal  
2517 is backed by analyses over several human datasets and a large dataset in mice.

2518 Despite its strong empirical contribution, the paper seems limited by the fact  
2519 that alternative computational hypotheses are not adequately considered (or at  
2520 least considered in a systematic way). At the same time, and although the paper  
2521 is well written, some parts are overly technical.

2522 We would like to thank the Reviewer for the very helpful comments on our manuscript.  
2523 We fully agree that the previous version of our manuscript did not consider alternative  
2524 computational hypotheses in a systematic and adequate way. As we outline in more detail in  
2525 our point-by-point-responses below, we have addressed this issue by adding a formal model  
2526 comparison of the bimodal inference model to reduced models, including a normative models  
2527 of Bayesian evidence accumulation. We have added null-hypothesis-testing for enhanced  
2528 history-congruence during internal mode. We have also moved a number of defensive analyses  
2529 to the Supplement.

2530 **Major comments:**

2531 **10.3.1 Comment 1**

2532 The authors collapse across various datasets in which different tasks were em-  
2533 ployed. However, some details on the nature of these different tasks and a  
2534 discussion on the rationale of collapsing behavioral metrics across them is miss-  
2535 ing. The authors mention that all tasks involved binary perceptual decisions. In  
2536 some parts of the manuscript the term “false alarms” is mentioned, indicating a  
2537 detection protocol. Other terms in the methods section (e.g., “set size”) might

2538 **need further clarification. Importantly, it is not clear how reaction times were**  
2539 **calculated in the various tasks and whether some experiments involved free**  
2540 **response paradigms while others interrogation/ cued paradigms (in which case**  
2541 **RTs can be defined as the latency between the response cue and the response).**

2542 We would like to thank the Reviewer for this important point. Regarding the rationale for  
2543 collapsing across the studies in the Confidence database: Having found strong evidence of  
2544 apparent between-mode fluctuations in a study on intermittent bistable perception<sup>19</sup>, our  
2545 goal was to test whether between-mode fluctuations were a general phenomenon in perceptual  
2546 decision-making. We thus had a lenient threshold for including studies from the Confidence  
2547 database, i.e., all that addressed the domain of perception in 2AFC tasks. This has the  
2548 advantage of looking at perceptual 2AFC decisions in general and indicated that history  
2549 effects and bimodal inference are present in a wide variety of tasks.

2550 At the same time, collapsing across diverse set of experiments means that the stimuli, the  
2551 timing and the way that responses were collected differed between them. To account for this  
2552 variability, we included individual experiments as random factors in linear mixed modeling.  
2553 We also made sure that perceptual performance is comparable across studies (Supplemental  
2554 Figure S1A-B). While our analysis of the IBL database was mainly motivated by investigating  
2555 bimodal inference across species, it also allowed us to replicate our results in a highly  
2556 standardized task that was collected across many individual subjects<sup>21</sup>. We have added the  
2557 rationale for collapsing across studies with its advantages and disadvantages to the *Open*  
2558 *questions and limitations* subsection of the discussion:

- 2559 • Our results suggest bimodal inference as a pervasive aspect of perceptual decision-making  
2560 in humans and mice. However, a number of limitations and open questions have to  
2561 be considered: First, this work sought to understand whether fluctuations between  
2562 internal and external mode, which we initially observed in an experiment on bistable  
2563 perception in humans<sup>19</sup>, represent a general phenomenon that occurs across a diverse

2564 set of perceptual decision-making tasks. Our analysis of the Confidence database<sup>20</sup>  
2565 therefore collapsed across all available experiments on binary perceptual decision-making.  
2566 Individual experiments differed with respect to the stimuli, the manipulation of difficulty,  
2567 the timing of trials, and the way responses were collected, but were highly comparable  
2568 with respect to the central variables of stimulus- and history-congruence (Supplemental  
2569 Figure S1A-B).

- 2570 • The variability across experiments, which we considered as random effects in all statistical  
2571 analyses, enabled us to assess whether bimodal inference represents a general phenomenon  
2572 in perceptual decision-making, but limited the precision at which we were able to  
2573 investigate the relation of mode to behavioral variables such as timing, task difficulty,  
2574 RT or confidence. This issue is partially resolved by our analyses of the IBL database,  
2575 which replicated our findings in an experiment that was highly standardized with respect  
2576 to timing, task difficulty, and behavioral read-out<sup>21</sup>. It will be an important task for  
2577 future research to validate our results on bimodal inference in a standardized dataset of  
2578 comparable volume in humans, which is, to our knowledge, not yet available.

2579 We apologize for the lack of clarity regarding the way we queried the Confidence database.  
2580 To select a broad variety of experiments on 2AFC perceptual decision-making, we queried  
2581 the Confidence database for studies from the *perception* category (excluding studies from the  
2582 categories *cognitive*, *motor*, *memory* and *mixed*) and selected studies with 2AFC responses.  
2583 Our previous version of the manuscript had mentioned the variable names given to the  
2584 difficulty variable in the individual experiments (i.e., the name of the column in the individual  
2585 .txt files provided for every experiment in the Confidence database). The term *false alarm*  
2586 turned up in the discussion of lapses of attention and arousal, which we have re-written in  
2587 response to Comment 19 by Reviewer 1 and Comment 6 by Reviewer 3. We now provide  
2588 more information on the experiments and variables selected in the Method section:

- 2589 • We downloaded the human data from the Confidence database<sup>20</sup> on 10/21/2020, limiting

2590 our analyses to the category *perception*. Within this category, we selected studies in  
2591 which participants made binary perceptual decisions between two alternatives. We  
2592 excluded two experiments in which the average perceptual accuracy fell below 50%.  
2593 After excluding these experiments, our sample consisted of 21.05 million trials obtained  
2594 from 4317 human participants and 66 individual experiments (Supplemental Table 1).  
2595 Out of the 66 included experiments, 62 investigated visual, 1 auditory, 2 proprioceptive,  
2596 and 1 multimodal perception. 59 experiments were based on discrimination and 6 on  
2597 detection, with one investigating both.

- 2598 • Out of the 58 experiments that provide information on RTs, 46 cued the response by the  
2599 onset of a response screen or an additional response cue, whereas 14 allowed participants  
2600 to respond at any time after stimulus onset.
- 2601 • 21 of the 66 included experiments used fixed difficulty levels, whereas 45 manipulated  
2602 difficulty levels within participants. Difficulty was manipulated via noise masks, contrast,  
2603 luminance, presentation time, or stimulus probability for gabor, dot coherence for  
2604 random dot kinematograms, difference in elements and set size for comparisons of  
2605 numerosity, difference in clicks for auditory discrimination, temporal distance for meta-  
2606 contrast masking, and amount of self-motion for proprioception. We treated task  
2607 difficulty as a missing variable for the experiments that fixed it at the participant-level,  
2608 as this precluded the computation of autocorrelation curves.

### 2609 10.3.2 Comment 2

2610 **The key premise that when participants do not rely on the external stimulus**  
2611 **they rely more on the previous trial needs to be more clearly (and statistically)**  
2612 **contrasted against a null hypothesis. For instance, an null hypothesis could be**  
2613 **that when participants place a lower weight on the stimulus they simply choose**  
2614 **randomly. It is important to specify a null hypothesis such that the key premise**  
2615 **does not appear self-evident or circular.**

<sup>2616</sup> We would like to thank the reviewer for highlighting this important point. Following this  
<sup>2617</sup> suggestion, we have explicitly tested our main hypothesis ( $H_1$ : periods of reduced stimulus-  
<sup>2618</sup> congruence are periods of enhanced reliance on history-congruence) against the following null  
<sup>2619</sup> hypotheses:

- <sup>2620</sup> •  $H_{01}$ : Periods of reduced stimulus-congruence are periods of enhanced random choices  
<sup>2621</sup> •  $H_{02}$ : Periods of reduced stimulus-congruence are periods of enhanced general bias

<sup>2622</sup> We present three sets of statistical analyses to test  $H_1$  against  $H_{01/2}$ :

<sup>2623</sup> First, we used logistic regression to predict individual choices. Under  $H_1$ , one would expect a  
<sup>2624</sup> significant effect of perceptual history in a logistic regression model that predicts individual  
<sup>2625</sup> choices from the external stimulus, perceptual history and general response bias. At the  
<sup>2626</sup> model level, one would expect higher AIC in a model without perceptual history as a predictor  
<sup>2627</sup> of individual choices, indicating that perceptual history influences choices beyond noise ( $H_{01}$ )  
<sup>2628</sup> and general response bias ( $H_{02}$ ).

<sup>2629</sup> In both humans and mice, we found a significant effect of perceptual history on choices  
<sup>2630</sup> while controlling for bias. When eliminating perceptual history as a predictor of individual  
<sup>2631</sup> choices, we found higher AIC (providing model-level evidence against  $H_{01}$  and  $H_{02}$ ). We  
<sup>2632</sup> complemented this analysis by computing AIC in individual observers (Supplemental Figure  
<sup>2633</sup> S4), and again found higher AIC in models from which perceptual history was eliminated.

<sup>2634</sup> We have made the following changes to the main manuscript:

<sup>2635</sup> Humans:

- <sup>2636</sup> • Subsection title: Fluctuations between internal and external mode cannot be reduced to  
<sup>2637</sup> general response biases or random choices
- <sup>2638</sup> • The core assumption of bimodal inference - that ongoing changes in the sensitivity to  
<sup>2639</sup> external information are driven by internal predictions induced via perceptual history

2640 - needs to be contrasted against two alternative hypotheses: When making errors,  
2641 observers may not engage with the task and respond stereotypically, i.e., exhibit stronger  
2642 general biases toward one of the two potential outcomes, or simply choose randomly.  
2643 Logistic regression confirmed that perceptual history made a significant contribution to  
2644 perception ( $\beta = 0.11 \pm 5.79 \times 10^{-3}$ ,  $z = 18.53$ ,  $p = 1.1 \times 10^{-76}$ ) over and above the  
2645 ongoing stream of external sensory information ( $\beta = 2.2 \pm 5.87 \times 10^{-3}$ ,  $z = 375.11$ ,  $p <$   
2646  $2.2 \times 10^{-308}$ ) and general response biases toward ( $\beta = 15.19 \pm 0.08$ ,  $z = 184.98$ ,  $p <$   
2647  $2.2 \times 10^{-308}$ ). When eliminating perceptual history as a predictor of individual choices  
2648 at individual trials, AIC increased by  $\delta_{AIC} = 1.64 \times 10^3$  (see Supplemental Figure S4A-B  
2649 for parameter- and model-level inference at the level of individual observers).

2650 Mice:

2651 • In line with humans, mice were biased toward perceptual history in  $54.03\% \pm 0.17\%$   
2652 of trials ( $T(163) = -7.52$ ,  $p = 3.44 \times 10^{-12}$ ; Figure 4A and Supplemental Figure S1D).  
2653 Perceptual history effects remained significant ( $\beta = 0.51 \pm 4.49 \times 10^{-3}$ ,  $z = 112.84$ ,  $p <$   
2654  $2.2 \times 10^{-308}$ ) when controlling for external sensory information ( $\beta = 2.96 \pm 4.58 \times 10^{-3}$ ,  
2655  $z = 646.1$ ,  $p < 2.2 \times 10^{-308}$ ) and general response biases toward one of the two potential  
2656 outcomes ( $\beta = -1.78 \pm 0.02$ ,  $z = -80.64$ ,  $p < 2.2 \times 10^{-308}$ ). When eliminating perceptual  
2657 history as a predictor of individual choices, AIC increased by  $\delta_{AIC} = 1.48 \times 10^4$ , arguing  
2658 against the notion that choice randomness and general response bias are the only  
2659 determinants of perceptual performance (see Supplemental Figure S4C-D for parameter-  
2660 and model-level inference within individual mice).

2661 Second, we analyzed dynamic changes in history- and stimulus-congruence (i.e., smoothed  
2662 probabilities for stimulus-congruence, history-congruence and general response bias in sliding  
2663 10 trial time-windows). Under H1, one would expect a significant negative correlation between  
2664 the dynamic probability of stimulus- and history-congruence. At the model level, one would

2665 expect higher AIC in a model without history-congruence as a predictor of stimulus-congruence,  
2666 indicating that changes in the probability of history-congruence influence stimulus-congruence  
2667 beyond noise ( $H0_1$ ) and general response bias ( $H0_2$ ).

2668 In both humans and mice, we found a significant negative correlation between history-  
2669 congruence and stimulus-congruence while controlling for general response bias. When elimi-  
2670 nating the dynamic probability of history-congruence as a predictor of stimulus-congruence,  
2671 we found higher AIC (providing model-level evidence against  $H0_1$  and  $H0_2$ ). The section  
2672 5.4 or our original manuscript (*Fluctuations between internal and external mode modulate*  
2673 *perceptual performance beyond the effect of general response biases*) complements these control  
2674 analyses and has been moved to the Supplement to stream-line the manuscript (following the  
2675 Comment 12 by Reviewer 1 and Comment 9 by Reviewer 3). We have modified the main  
2676 manuscript in the following way:

2677 Humans:

2678 • Finally, we ensured that fluctuations in stimulus- and history-congruence are linked to  
2679 each other, while controlling for fluctuations in the strength of general response biases.

2680 When perceptual choices were less biased toward external information, participants  
2681 relied more strongly on internal information acquired from perceptual history (and vice  
2682 versa,  $\beta = -0.05 \pm 5.63 \times 10^{-4}$ ,  $T(2.1 \times 10^6) = -84.21$ ,  $p < 2.2 \times 10^{-308}$ ), controlling  
2683 for fluctuations in the strength of general response biases ( $\beta = -0.06 \pm 5.82 \times 10^{-4}$ ,  
2684  $T(2.1 \times 10^6) = -103.51$ ,  $p < 2.2 \times 10^{-308}$ ).

2685 • (...) Likewise, eliminating the dynamic fluctuations in history-congruence as a predictor  
2686 of fluctuations in stimulus-congruence yielded an increase in AIC by  $\delta_{AIC} = 7.06 \times 10^3$ .  
2687 These results provided model-level evidence against the null hypotheses that fluctuations  
2688 in stimulus-congruence are driven exclusively by choice randomness or general response  
2689 bias (see Supplemental Section 9.2 for an in-depth assessment of general response bias).

2690 Mice:

- 2691 • As in humans, fluctuations in the strength of history-congruent biases had a significant  
2692 effect on stimulus-congruence ( $\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$ ,  $T(1.34 \times 10^6) = -168.39$ ,  $p <$   
2693  $2.2 \times 10^{-308}$ ) beyond the effect of ongoing changes in general response biases ( $\beta_2 = -0.03$   
2694  $\pm 6.94 \times 10^{-4}$ ,  $T(1.34 \times 10^6) = -48.14$ ,  $p < 2.2 \times 10^{-308}$ ). Eliminating the dynamic  
2695 fluctuations in history-congruence as a predictor of fluctuations in stimulus-congruence  
2696 resulted in an increase in AIC by  $\delta_{AIC} = 2.8 \times 10^4$ . This confirmed that, in both humans  
2697 and mice, perceptual performance is modulated by systematic fluctuations between  
2698 externally- and internally-oriented modes of sensory processing that exist beyond general  
2699 response bias (see Supplemental Section 9.2 for an in-depth assessment of general  
2700 response bias).

2701 Third, we analyzed full and history-conditioned psychometric curves in external and internal  
2702 mode as well as across modes. Under our main hypothesis that periodic reductions in  
2703 sensitivity to external information are driven by increases in the impact of perceptual history,  
2704 one would expect (i) a history-dependent increase in biases and lapses (effects of perceptual  
2705 history), and (ii), a history-independent increase in threshold (reduced sensitivity to external  
2706 information). Conversely, if what we identified as internal mode processing was in fact driven  
2707 by random choices, one would expect (i), a history-independent increase in lapses (choice  
2708 randomness), (ii), no change in bias (no effect of perceptual history), and (iii), reduced  
2709 thresholds (reduced sensitivity to external information). In both humans and mice, we  
2710 observed the pattern predicted by H1. In response to the comments by Reviewer 1 and 3,  
2711 we have significantly streamlined the manuscript and moved our assessment of psychometric  
2712 functions to the Supplement. We now provide a summary of our results in the main manuscript  
2713 to make our reasoning with respect to  $H0_1$  and  $H1$  more explicit:

2714 Humans:

2715 • To confirm that changes in the sensitivity to external information are indicative of  
2716 internal mode processing, we estimated full and history-dependent psychometric curves  
2717 during internal, external, and across modes. If, as we hypothesized, internal mode  
2718 processing reflects an enhanced impact of perceptual history, one would expect a history-  
2719 dependent increase in biases and lapses as well as a history-independent increase in  
2720 threshold. Conversely, if internal mode processing were driven by random choices, one  
2721 would expect a history-independent increase in lapses and threshold, and no change in  
2722 bias. In line with our prediction, we found that internal mode processing was associated  
2723 with a history-dependent increase in bias and lapse as well as a history-independent  
2724 increase in threshold (Supplemental Section 9.3.1 and Supplemental Figure S6). This  
2725 confirms that internal mode processing is indeed driven by an enhanced impact of  
2726 perceptual history.

2727 Mice:

2728 • When fitting full and history-conditioned psychometric curves to the data from the IBL  
2729 database, we observed that internal mode processing was associated with a history-  
2730 dependent increase in bias and lapse as well as a history-independent increase in threshold  
2731 (Supplemental Section 9.3.2 and Supplemental Figure S7). This provided further evidence  
2732 for the hypothesis that internal mode processing is driven by an enhanced impact of  
2733 perceptual history, as opposed to increased choice randomness.

2734 **10.3.3 Comment 3**

2735 **From a mechanistic (sequential sampling) perspective, several previous papers**  
2736 **have examined whether choice history biases influence the starting point or the**  
2737 **drift rate of the evidence accumulation process. Under the former formulation,**  
2738 **reliance on the evidence vs. reliance on the previous choice will be naturally**  
2739 **anti-correlated (the less weight you place on the evidence the more impactful the**

choice history will be, assuming that the last choice is represented as a starting point bias). This seems to be mapping onto the computational model the authors describe, in which there is a weight on the prior, a weight on the likelihood and the assumption that these weights fluctuate in anti-phase. It is not obvious that this anti-phase relationship needs to be imposed ad-hoc. Or whether it would emerge naturally (using a mechanistic or Bayesian framework). More generally, the authors assert that without an external mechanism prior biases would be impossible to overcome, and this would misfit the data. However, it would be important to a) actually show that the results cannot be explained by a single mechanism in which the anti-phase relationship is emergent rather than ad-hoc, b) relate the current framework with previous mechanistic considerations of serial choice biases.

We would like to thank the reviewer for pointing this out. We agree that both normative Bayesian and mechanistic drift diffusion are bound to lead to anti-correlated effects of sensory information and perceptual history *at the level of individual trials*. This, however, does not necessarily entail slow fluctuations in the impact of sensory information and perceptual history that evolve *over many consecutive trials*. We now provide a systematic model comparison and discuss our model in relation to drift diffusion models and descriptive models that assume slow changes in the latent parameters underlying perceptual decision-making (such as Roy et al., Neuron 2021 or Ashwood et al. Nature Neuroscience et al. 2022). We also discuss the ad-hoc nature of the bimodal inference model in the subsection *Limitations and open questions*.

- We used a maximum likelihood procedure to fit the bimodal inference model (M1, Figure 1F) to the behavioral data from the Confidence database<sup>20</sup> and the IBL database<sup>21</sup>, optimizing the parameters  $\alpha$ ,  $H$ ,  $amp_{LLR}$ ,  $amp_\psi$ ,  $f$ ,  $p$ , and  $\zeta$  (see Methods for details and Supplemental Table T2 for a summary of the parameters of the bimodal inference model).

2766 We validated our model in three steps: First, to show that bimodal inference does not  
2767 emerge spontaneously in normative Bayesian models of evidence accumulation, but  
2768 requires the ad-hoc addition of anti-phase oscillations in prior and likelihood precision,  
2769 we compared the bimodal inference model to four control models (M2-5, Figure 1G).  
2770 In these models, we successively removed the anti-phase oscillations (M2-M4) and the  
2771 integration of information across trials (M5) from the bimodal inference model and  
2772 performed a model comparison based on AIC.

- 2773 • Model M2 ( $AIC_2 = 9.76 \times 10^4$  in humans and  $4.91 \times 10^4$  in mice) and Model M3 ( $AIC_3$   
2774  $= 1.19 \times 10^5$  in humans and  $5.95 \times 10^4$  in mice) incorporated only oscillations of either  
2775 likelihood or prior precision. Model M4 ( $AIC_4 = 1.69 \times 10^5$  in humans and  $9.12 \times 10^4$  in  
2776 mice) lacked any oscillations of likelihood and prior precision and corresponded to the  
2777 normative model proposed by Glaze et al.<sup>51</sup>. In model M5 ( $AIC_4 = 2.01 \times 10^5$  in humans  
2778 and  $1.13 \times 10^5$  in mice), we furthermore removed the integration of information across  
2779 trials, such that perception depended only in incoming sensory information (Figure 1G).
- 2780 • The bimodal inference model achieved the lowest AIC across the full model space ( $AIC_1$   
2781  $= 8.16 \times 10^4$  in humans and  $4.24 \times 10^4$  in mice) and was clearly superior to the normative  
2782 Bayesian model of evidence accumulation ( $\delta_{AIC} = -8.79 \times 10^4$  in humans and  $-4.87 \times 10^4$   
2783 in mice; Supplemental Figure S9).
- 2784 • In sum, computational modeling suggested that between-mode fluctuations are best  
2785 explained by two interlinked processes (Figure 1E): (i), the dynamic accumulation of  
2786 information across successive trials mandated by normative Bayesian models of evidence  
2787 accumulation and, (ii), ongoing anti-phase oscillations in the impact of external and  
2788 internal information.
- 2789 • Could bimodal inference emerge spontaneously in normative models of perceptual  
2790 decision-making? In predictive processing, the relative precision of prior and likelihood  
2791 determines their integration into the posterior that determines the content of perception.

2792 At the level of individual trials, the perceptual impact of internal predictions generated  
2793 from perceptual history (prior precision) and external sensory information (likelihood  
2794 precision) are thus necessarily anti-correlated. The same holds for mechanistic models of  
2795 drift diffusion, which understand choice history biases as driven by changes in the starting  
2796 point<sup>51</sup> or the drift rate of evidence accumulation<sup>32</sup>. Under the former formulation,  
2797 perceptual history is bound to have a stronger influence on perception when less weight  
2798 is given to incoming sensory evidence, assuming that the last choice is represented as a  
2799 starting point bias. The effects of choice history in normative Bayesian and mechanistic  
2800 drift diffusion models can be mapped onto one another via the Bayesian formulation  
2801 of drift diffusion<sup>60</sup>, where the inverse of likelihood precision determines the amount of  
2802 noise in the accumulation of new evidence, and prior precision determines the absolute  
2803 shift in its starting point<sup>60</sup>.

- 2804 • While it is thus clear that the impact of perceptual history and sensory evidence are anti-  
2805 correlated *at each individual trial*, we here introduce anti-phase oscillations as an ad-hoc  
2806 modification to model slow fluctuations in prior and likelihood precision that evolve *over*  
2807 *many consecutive trials* and are not mandated by normative Bayesian or mechanistic  
2808 drift diffusion models. The bimodal inference model provides a reasonable explanation  
2809 of the linked autocorrelations in stimulus- and history-congruence, as evidenced by  
2810 formal model comparison, successful prediction of RTs and confidence as out-of-training  
2811 variables, and a qualitative reproduction of our empirical data from posterior model  
2812 parameter as evidence against over- or under-fitting.
- 2813 • Of note, similar non-stationarities have been observed in descriptive models that assume  
2814 continuous<sup>61</sup> or discrete<sup>12</sup> changes in the latent states that modulate perceptual decision-  
2815 making at slow timescales. A recent computational study<sup>62</sup> has used a Hidden Markov  
2816 model to investigate perceptual decision-making in the IBL database<sup>21</sup>. In analogy  
2817 to our findings, the authors observed that mice switch between temporally extended

2818 *strategies* that last for more than 100 trials: During *engaged* states, perception was highly  
2819 sensitive to external sensory information. During *disengaged* states, in turn, choice  
2820 behavior was prone to errors due to enhanced biases toward one of the two perceptual  
2821 outcomes<sup>62</sup>. Despite the conceptual differences to our approach (discrete states in a  
2822 Hidden Markov model that correspond to switches between distinct decision-making  
2823 strategies<sup>62</sup> vs. gradual changes in mode that emerge from sequential Bayesian inference  
2824 and ongoing fluctuations in the impact of external relative to internal information), it is  
2825 tempting to speculate that engaged/disengaged states and between-mode fluctuations  
2826 might tap into the same underlying phenomenon.

- 2827 • A third open question concerns the computational underpinnings of bimodal inference.  
2828 The addition of slow anti-phase oscillations to the integration of prior and likelihood rep-  
2829 resents an ad-hoc modification of a normative Bayesian model of evidence accumulation<sup>51</sup>.  
2830 While the bimodal inference model is supported by formal model comparison, the suc-  
2831 cessful prediction of out-of-training variables and the qualitative reproduction of our  
2832 empirical data in simulations from posterior model parameters, it is an important task for  
2833 future research to test (i), whether between-mode fluctuations can emerge spontaneously  
2834 in hierarchical models of Bayesian inference, (ii), whether modes are continuous<sup>19</sup> or  
2835 discrete<sup>62</sup>, and (iii), whether bimodal inference can be causally manipulated by ex-  
2836 perimental variables. We speculate that between-mode fluctuations may separate the  
2837 perceptual contribution of internal predictions and external sensory data in time, creating  
2838 unambiguous learning signals that benefit inference about the precision of prior and  
2839 likelihood, respectively. This proposition should be tested empirically by relating the  
2840 phenomenon of bimodal inference to performance in, e.g., reversal learning, probabilistic  
2841 reasoning, or metacognition.

2842 **10.3.4 Comment 4**

2843 The authors need to unpack their definition of history biases since in previous  
2844 work biases due to the response or the identity of the stimulus at the previous  
2845 trial are treated differently. Here, the authors focus on response biases but it  
2846 is not clear whether they could examine also stimulus-driven history biases (in  
2847 paradigms where stimulus-response is remapped on each trial).

2848 We would like to thank the reviewer for raising this important point. We defined the  
2849 history-biases reported in our main manuscript by comparing the *response about the perceived*  
2850 stimulus category (A vs. B) at the current and at the preceding trial (choice history). An  
2851 alternative would have been to define history biases by comparing the choice at the current  
2852 trial to the stimulus category *presented* at the preceding trial (stimulus history). As we show  
2853 below, perceptual responses tended to be biased not only toward choice history, but also (but  
2854 to a lesser degree) to stimulus history. This is expected, as perception was *stimulus-congruent*  
2855 on approximately 75% of trials, causing the effects of the preceding response and the preceding  
2856 stimulus to be highly correlated. We therefore compared the effects on choice history and  
2857 stimulus history induced by trials at which perception was *stimulus-incongruent*, since those  
2858 trials lead to opposite predictions regarding the perceptual choice at the subsequent trial.

2859 As expected, perceptual choices were attracted toward perceptual choices at preceding  
2860 stimulus-incongruent trials (i.e., a positive effect of choice history). By contrast, perceptual  
2861 choices tended to be repelled away from the stimulus presented the preceding trial. This  
2862 repulsion of choices away from stimuli presented at stimulus-incongruent trials confirms  
2863 that the choices at stimulus-incongruent trials were the primary driver of serial effects in  
2864 perception in both humans and mice.

2865 We now refer to our analysis on stimulus history as an additional confound, which we present  
2866 in detail in the Supplement 9.1 of our manuscript:

- 2867 • (...) These serial biases were effects of choice history, i.e., driven by the experiences  
2868 reported at the preceding trial, and could not be attributed to stimulus history, i.e., to  
2869 effects of the stimuli presented at the preceding trial (Supplemental Section 9.1).

2870 Supplement:

- 2871 • The main manuscript reports the effects of perceptual history, which we defined as the  
2872 impact of the choice at the preceding trial on the choice at the current trial (henceforth  
2873 *choice history*). *Stimulus history*, which is defined as the impact of the stimulus presented  
2874 at the preceding trial on the choice at the present trial, represents an alternative approach  
2875 to this. Here, we compare the effects of choice history to the effects of stimulus history.
- 2876 • We observed a significant bias toward stimulus history (humans:  $49.76\% \pm 0.1\%$  of trials,  
2877  $\beta = 1.26 \pm 0.94$ ,  $T(373.62) = 1.34$ ,  $p = 0.18$ ; mice:  $51.11\% \pm 0.08\%$  of trials,  $T(164)$   
2878  $= 13.4$ ,  $p = 3.86 \times 10^{-28}$ ). The bias toward stimulus history was smaller than the bias  
2879 toward choice history (humans:  $\beta = -3.53 \pm 0.5$ ,  $T(66.53) = -7.01$ ,  $p = 1.48 \times 10^{-9}$ ;  
2880 mice:  $T(164) = -17.21$ ,  $p = 1.43 \times 10^{-38}$ ).
- 2881 • The attraction of choices toward both preceding choices and stimuli is expected, as  
2882 perception was *stimulus-congruent* on approximately 75% of trials, causing choices and  
2883 stimuli to be highly correlated. We therefore compared the effects of choice history and  
2884 stimulus history after *stimulus-incongruent* (i.e., *error*) trials, since those trials lead to  
2885 opposite predictions regarding the perceptual choice at the subsequent trial.
- 2886 • As expected from the findings presented in the main manuscript, perceptual choices were  
2887 attracted toward perceptual choices when the inducing trial was stimulus-incongruent  
2888 (i.e., a positive effect of choice history; humans:  $\beta = 0.19 \pm 1.4 \times 10^{-4}$ ,  $z = 1.36 \times 10^3$ ,  $p <$   
2889  $2.2 \times 10^{-308}$ ; mice:  $\beta = 0.92 \pm 0.01$ ,  $z = 88.82$ ,  $p < 2.2 \times 10^{-308}$ ). By contrast, perceptual  
2890 choices tended to be repelled away from the stimulus presented at preceding stimulus-  
2891 incongruent trial (i.e., a negative effect of stimulus history; humans:  $\beta = -0.19 \pm 0.01$ ,

2892  $z = -16.47$ ,  $p = 5.99 \times 10^{-61}$ : mice:  $\beta = -0.92 \pm 0.01$ ,  $z = -88.76$ ,  $p < 2.2 \times 10^{-308}$ ).

2893 This repulsion of choices away from stimuli presented at stimulus-incongruent trials  
2894 confirmed that choices (which are anti-correlated to stimuli at stimulus-incongruent  
2895 trials) were the primary driver of attracting serial effects in perception.

- 2896 • In sum, the above results suggest that, in both humans and mice, serial dependencies  
2897 were better explained by the effects of choice history as opposed to the effects of stimulus  
2898 history. This aligns with a result recently published for the IBL database, where mice  
2899 were shown to follow an *action-kernel* as opposed to a *stimulus-kernel* model when  
2900 integrating information across trials<sup>81</sup>.

2901 **10.3.5 Comment 5**

2902 Previous work, which the authors acknowledges in their Discussion (6.5), distin-  
2903 guishes repetitive history biases from alternating biases. For instance, in Braun,  
2904 Urai & Donner (2018, JoN) participants are split into repetitive or alternating.  
2905 Shouldn't the authors define the history bias in a similar fashion? The authors  
2906 point out that attracting and repelling biases operate simultaneously across  
2907 different timescales. However, this is not warranted given Braun et. al and other  
2908 similar papers. It is not clear how this more nuanced definition of history bias  
2909 would alter the conclusions.

2910 Our empirical results show that, on average, history biases tend to be repetitive (Figure 2A,  
2911 Figure 3A, and the biases in the psychometric functions in the Supplemental Figure S6-7).  
2912 In fact, only 2 of the 66 experiments we included from the Confidence database<sup>20</sup> showed  
2913 significant alternating biases (Supplemental Figure S1, please note that history-congruence  
2914 was not used in the inclusion algorithm). However, this does not rule out the possibility that  
2915 there are periods of alternating biases in the other experiments with net repeating effects.

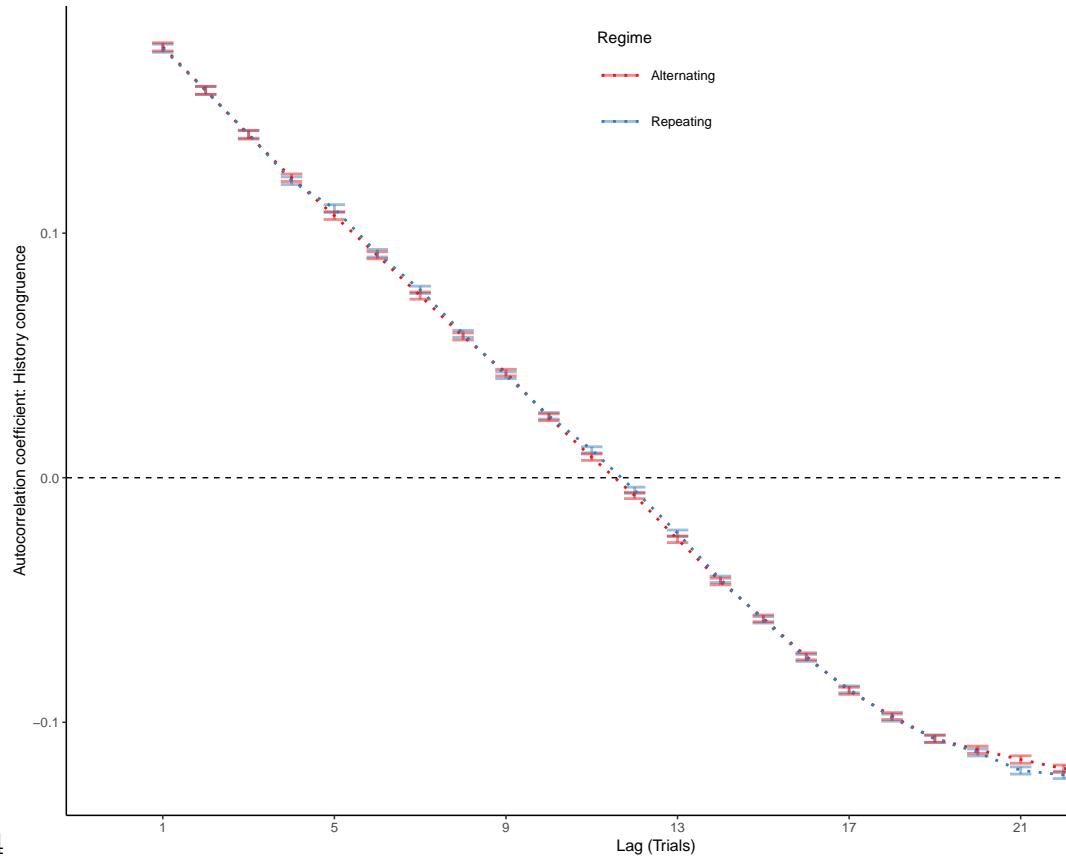
2916 Importantly, our central finding of autocorrelation in history-congruence does not distinguish

2917 between alternating and repetitive history biases. In the plot below, we show autocorrelation  
2918 curves for fluctuations in history-congruence for both alternation (hazard = 0.8) and repetition  
2919 (hazard = 0.2). Both were simulated for 10 blocks of a random duration between 15  
2920 and 30 trials, interleaved with 10 blocks with no history biases (hazard = 0.5). This  
2921 simulation illustrates that the autocorrelation of alternating and repeating biases is identical  
2922 for symmetric pairs of hazard rates. The autocorrelation of history-congruence and the  
2923 associated internal mode processing is therefore not tied to repeating biases, but accommodates  
2924 alternating biases as well (which seem to be, on average and in our data, less frequent). We  
2925 therefore did not separate alternating from repeating biases in our analysis of mode.

2926 We apologize for not having recognized this aspect in the previous version of the discussion.  
2927 We have rewritten the paragraph on alternating and repeating biases in the discussion,  
2928 referring to the plot below, which we have added to the Supplemental Materials.

2929 • Second, our results point to an attraction of perception toward preceding choices.  
2930 Previous work has shown that perceptual decision-making is concurrently affected by  
2931 both attractive and repulsive serial biases that operate on distinct time-scales and  
2932 serve complementary functions for sensory processing<sup>27,75,76</sup>: Short-term attraction may  
2933 serve the decoding of noisy sensory inputs and increase the stability of perception,  
2934 whereas long-term repulsion may enable efficient encoding and sensitivity to change<sup>27</sup>.  
2935 In the data analyzed here, history biases tended to be repetitive (Figure 2A, Figure 3A,  
2936 Supplemental Figure S6 and S7), and only 2 of the 66 experiments of the Confidence  
2937 database<sup>20</sup> showed significant alternating biases (Supplemental Figure S1). However,  
2938 as we show in Supplemental Figure S14, fluctuations in both alternating and repeating  
2939 history biases generate overlapping autocorrelation curves. Our analysis of between-mode  
2940 fluctuations is therefore not tied exclusively to repeating biases, but accommodates  
2941 alternating biases as well, such that both may lead to internally-biased processing  
2942 and reduced sensitivity to external sensory information. Future work could apply our

2943 approach to paradigms that boost alternating as opposed to repeating biases, as this  
2944 would help to better understand how repetition and alternation are linked in terms of  
2945 their computational function and neural implementation<sup>27</sup>.



2946 **Supplemental Figure S14**

- 2947 • **Supplemental Figure S14.** Autocorrelation of history-congruence of alternating and  
2948 repeating biases. Here, we simulate the autocorrelation of history-congruence in  $10^3$   
2949 synthetic participants. In the repeating regime (blue), history-congruence fluctuated  
2950 between 50% and 80% (blue) in interleaved blocks (10 blocks per condition with a  
2951 random duration between 15 and 30 trials). In the alternation regime (red), history-  
2952 congruence fluctuated between 50% and 20%. The resulting autocorrelation curves for  
2953 history-congruence overlap, indicating that our analysis is able to accommodate both  
2954 repeating and alternating biases.

2955 **10.3.6 Comment 6**

2956 The arousal hypothesis seems to be ruled out too easily, merely in the presence  
2957 of a non-monotonic “state” vs. RT pattern. Arousal can have an inverted U-  
2958 shaped effect on behavioral performance and recent paper has demonstrated  
2959 a non-monotonic effect of tonic arousal (baseline pupil) on RTs and accuracy  
2960 (<https://www.biorxiv.org/content/10.1101/2023.07.28.550956.abstract>). More  
2961 generally, the RT and confidence analyses need to be complemented, perhaps by  
2962 computational modeling using sequential sampling models, as these behavioral  
2963 metrics have multiple mechanistic mappings (e.g., a fast RT might correspond to  
2964 high SNR or an impulsive decisions driven by a starting point bias).

2965 We would like to thank the reviewer for this important point. Considering this Comment  
2966 and the Comment 3 by Reviewer 1, we realize that the quadratic relationships between  
2967 mode and RTs/confidence do not represent a convincing defensive analysis against the  
2968 potential contributions of arousal to the phenomenon that we have identified as between-  
2969 mode fluctuations. Rather, we now interpret the fluctuations of RTs/confidence with mode  
2970 as indicative of a scenario in which between-mode fluctuations modulate a decision-variable  
2971 that determines not only the perceptual choices, but also the speed and confidence at which  
2972 they are made.

2973 Therefore, as a first response to this comment, we have re-phrased our assessment of RT and  
2974 confidence in the following way:

2975 Humans:

- 2976 • The above results point to systematic fluctuations in the *decision variable*<sup>44</sup> that deter-  
2977 mines perceptual choices, causing enhanced sensitivity to external stimulus information  
2978 during external mode and increased biases toward preceding choices during internal  
2979 mode. As such, fluctuations in mode should influence downstream aspects of behavior

2980 and cognition that operate on the perceptual decision variable<sup>44</sup>. To test this hypothesis  
2981 with respect to motor behavior and metacognition, we asked how bimodal inference  
2982 relates to response times (RTs) and confidence reports. (...).

- 2983 • (...) In sum, the above results indicate that reporting behavior and metacognition do  
2984 not map linearly onto the mode of sensory processing. Rather, they suggest that slow  
2985 fluctuations in the respective impact of external and internal information are most likely  
2986 to affect perception at an early level of sensory analysis<sup>46,47</sup>. Such low-level processing  
2987 may thus integrate perceptual history with external inputs into a decision variable<sup>44</sup>  
2988 that influences not only perceptual choices, but also the speed and confidence at which  
2989 they are made.
- 2990 • In what follows, we probe alternative explanations for between-mode fluctuations, test  
2991 for the existence of modes in mice, and propose a predictive processing model that  
2992 explains fluctuations in mode ongoing shifts in the precision afforded to external sensory  
2993 information relative to internal predictions driven by perceptual history.

2994 Mice:

- 2995 • The above results confirm that fluctuations between internally- and externally-biased  
2996 modes generalize to perceptual decision-making in mice. As in humans, we hypothesized  
2997 that bimodal inference modulates the decision variable<sup>44</sup> that determines not only  
2998 perceptual choices, but also downstream aspects of mouse behavior<sup>44</sup>. (...). When  
2999 fitting full and history-conditioned psychometric curves to the data from the IBL  
3000 database, we observed that internal mode processing was associated with a history-  
3001 dependent increase in bias and lapse as well as a history-independent increase in threshold  
3002 (Supplemental Section 9.3.2 and Supplemental Figure S7). Over time, the frequency of  
3003 history-congruent choices increased alongside stimulus-congruence and speed of response  
3004 as mice were exposed to the experiment, arguing against the proposition that biases

3005 toward perceptual history reflected an unspecific response strategy in mice who were  
3006 not sufficiently trained on the IBL task.

3007 Second, we have re-structured the section of defensive analyses, where we contrast the  
3008 phenomenon that we identify as fluctuating modes in perception with stereotypical or random  
3009 responses as evidence of low task engagement, and not specifically with attention or arousal,  
3010 which we discuss below. To streamline the manuscript, we report those analyses in detail in  
3011 the Supplement (see Comments 12 by Reviewer 1 and Comment 9 by Reviewer 3).

3012 • The core assumption of bimodal inference - that ongoing changes in the sensitivity to  
3013 external information are driven by internal predictions induced via perceptual history  
3014 - needs to be contrasted against two alternative hypotheses: When making errors,  
3015 observers may not engage with the task and respond stereotypically, i.e., exhibit stronger  
3016 general biases toward one of the two potential outcomes, or simply choose randomly.  
3017 Logistic regression confirmed that perceptual history made a significant contribution to  
3018 perception ( $\beta = 0.11 \pm 5.79 \times 10^{-3}$ ,  $z = 18.53$ ,  $p = 1.1 \times 10^{-76}$ ) over and above the  
3019 ongoing stream of external sensory information ( $\beta = 2.2 \pm 5.87 \times 10^{-3}$ ,  $z = 375.11$ ,  $p <$   
3020  $2.2 \times 10^{-308}$ ) and general response biases toward ( $\beta = 15.19 \pm 0.08$ ,  $z = 184.98$ ,  $p <$   
3021  $2.2 \times 10^{-308}$ ).

3022 • When eliminating perceptual history as a predictor of individual choices at individual  
3023 trials, AIC increased by  $\delta_{AIC} = 1.64 \times 10^3$  (see Supplemental Figure S4A-B for parameter-  
3024 and model-level inference at the level of individual observers). Likewise, when eliminating  
3025 slow fluctuations in history-congruence as a predictor of slow fluctuations in stimulus-  
3026 congruence across trials, we observed an increase in AIC by  $\delta_{AIC} = 7.06 \times 10^3$ . These  
3027 results provided model-level evidence against the null hypotheses that fluctuations in  
3028 stimulus-congruence are driven exclusively by choice randomness or general response  
3029 bias (see Supplemental Section 9.2 for an in-depth assessment of general response bias).

- 3030 • To confirm that changes in the sensitivity to external information are indicative of  
3031 internal mode processing, we estimated full and history-dependent psychometric curves  
3032 during internal, external, and across modes. If, as we hypothesized, internal mode  
3033 processing reflects an enhanced impact of perceptual history, one would expect a history-  
3034 dependent increase in biases and lapses as well as a history-independent increase in  
3035 threshold. Conversely, if internal mode processing were driven by random choices, one  
3036 would expect a history-independent increase in lapses and threshold, and no change in  
3037 bias. In line with our prediction, we found that internal mode processing was associated  
3038 with a history-dependent increase in bias and lapse as well as a history-independent  
3039 increase in threshold (Supplemental Section 9.3 and Supplemental Figure S6-7). This  
3040 confirmed that internal mode processing is indeed driven by an enhanced impact of  
3041 perceptual history.
- 3042 • In line with this, the quadratic relationship between mode and confidence (Figure 2J)  
3043 suggested that biases toward internal information do not reflect a post-perceptual strategy  
3044 or repeating preceding choices when the subjective confidence in the perceptual decision  
3045 is low. Moreover, while responses became faster with longer exposure to the experiments  
3046 of the Confidence database, the frequency of history-congruent choices increased over  
3047 time, speaking against the proposition that participants may stereotypically repeat  
3048 preceding choices when not yet familiar with the experimental task (see Supplemental  
3049 Section).
- 3050 • Taken together, our results thus argue against recurring intervals of low task engagement,  
3051 which may be signaled by stereotypical or random responses, as an alternative explanation  
3052 for the phenomenon that we identify as bimodal inference.

3053 Third, in response the Comment 3 by Reviewer 1, we now interpret the quadratic relationship  
3054 of mode to RTs/confidence in the context of predictive processing views on attention<sup>53</sup>. Based  
3055 on the Bayesian formulation of drift diffusion<sup>60</sup>, we propose that the effects of likelihood on

3056 prior precision on the decision variable and, consequently, on confidence and RTs can be  
3057 translated into the mechanistic framework of drift diffusion. Specifically, Bitzer et al. relate  
3058 likelihood precision to noise in the accumulation process, and prior precision to the amount  
3059 of shift in the starting point<sup>60</sup>. As a third response to this comment, we have re-written  
3060 our discussion of the quadratic relationship of mode to RTs and Confidence, focusing on  
3061 predictive processing models attention, which we relate to mechanistic drift diffusion models:

- 3062 • How does attention relate to between-mode fluctuations? According to predictive  
3063 processing, attention corresponds to the precision afforded to the probability distributions  
3064 that underlie perceptual inference<sup>53</sup>. As outlined above, between-mode fluctuations  
3065 can be understood as ongoing shifts in the precision afforded to likelihood (*external*  
3066 *mode*) and prior (*internal mode*), respectively. When the precision afforded to prior or  
3067 likelihood increases, posterior precision increases, which leads to faster RTs and higher  
3068 confidence. When defined from the perspective of predictive processing as the precision  
3069 afforded to likelihood and prior<sup>53</sup>, fluctuations in attention may thus provide a plausible  
3070 explanation for the quadratic relationship of mode to RTs and confidence (Figure 2H  
3071 and J; Figure 3I; Figure 4I). Such effects of attention in the predictive processing sense  
3072 can be directly related to mechanistic drift diffusion models<sup>60</sup>, where both larger shifts  
3073 in starting point (related to increased prior precision in internal mode) and lower noise  
3074 in the accumulation of evidence (related to increased likelihood precision in external  
3075 mode) may explain faster and more confident responses.

3076 Given the correspondence between normative Bayesian and mechanistic drift diffusion  
3077 models<sup>60</sup>, we believe that we would not gain additional insights into the role of arousal  
3078 and additional potential confounds or causes of between-mode fluctuations by fitting drift  
3079 diffusion models as an alternative class of behavioral models to our data. To understand the  
3080 relation of arousal to the bimodal inference, we think that it is necessary to look at data  
3081 beyond behavior, such as pupillometry, video tracking of response behavior, or neural data.

3082 While this is beyond the scope of the current manuscript, we plan to do these analyses in  
3083 a follow-up paper, using data published by the IBL after this paper was submitted. The  
3084 IBL data now contains eye tracking, video tracking of response behavior, and neuropixel  
3085 recordings across the whole mouse brain<sup>71</sup>. As a fourth response to this comment, we have  
3086 re-written our discussion of attention and arousal:

- 3087 • Outside of the predictive processing field, attention is often understood in the context of  
3088 task engagement<sup>63</sup>, which varies according to the availability of cognitive resources that  
3089 are modulated by factors such as tonic arousal, familiarity with the task, or fatigue<sup>63</sup>. Our  
3090 results suggest that internal mode processing cannot be completely reduced to intervals  
3091 of low task engagement: In addition to shorter RTs and elevated confidence, choices  
3092 during internal mode were not random or globally biased, but driven by perceptual  
3093 history (Supplemental Figures S6-7). Moreover, our computational model identified  
3094 the dominant timescale of between-mode fluctuations at  $0.11\sqrt{1/N_{trials}}$ , which may be  
3095 compatible with fluctuations in arousal<sup>64</sup>, but is faster than to be expected for the  
3096 development of task familiarity or fatigue.
- 3097 • However, in interpreting the impact of between-mode fluctuations on perceptual accuracy,  
3098 speed of response and confidence, it is important to consider that global modulators  
3099 such as tonic arousal are known to have non-linear effects on task performance<sup>65</sup>: In  
3100 perceptual tasks, performance seems to be highest during mid-level arousal, whereas low-  
3101 and high-level arousal lead to reduced accuracy and slower responses<sup>65</sup>. This contrasts  
3102 with the effects of bimodal inference, where accuracy increases linearly as one moves  
3103 from internal to external mode, and responses become faster at both ends of the mode  
3104 spectrum.
- 3105 • Of note, high phasic arousal has been shown to suppress multi-domain biases in decision-  
3106 making in humans and mice<sup>66-68</sup>, including the biases toward perceptual history<sup>28</sup> that  
3107 we implicate in internal mode processing. The increase in response speed and history

3108 congruence over time (Supplemental Section 9.4) may argue against insufficient training  
3109 as an alternative explanation for internal mode processing, but may also taken as a  
3110 sign of waning arousal. The multiple mechanistic mappings to RTs and confidence  
3111 therefore warrant more direct measures of arousal (such as pupil size<sup>28,65,66,68–70</sup>, motor  
3112 behavior<sup>69,70</sup>, or neural data<sup>71</sup>) to better delineate bimodal inference from fluctuations  
3113 in global modulators of task performance.

3114 **10.3.7 Comment 7**

3115 **In several analysis the authors present an effect and then show that this effects**  
3116 **persists when key variables/ design aspects are also taken into account (see an**  
3117 **example at around line 70). It makes more sense to present only one single**  
3118 **analysis in which these key variables are controlled for. Results cannot be**  
3119 **interpreted if they are spurious factors driving them so it is not clear why some**  
3120 **of the results are presented in two versions (“uncontrolled” and “controlled”**  
3121 **analyses).**

3122 We apologize for this. We have updated our manuscript accordingly and have omitted,  
3123 whenever possible, reports of uncontrolled analyses (highlighted in the main text). The most  
3124 significant changes are summarized here:

- 3125 • Group-level autocorrelation curves in humans: In line with previous work<sup>8</sup>, we found that  
3126 the probability of stimulus-congruence was not independent across successive trials: At  
3127 the group level, stimulus-congruent perceptual choices were significantly autocorrelated  
3128 for up to 15 trials (Figure 2B), controlling for task difficulty and the sequence of presented  
3129 stimuli (Supplemental Figure 2A-B). (...) In close analogy to stimulus-congruence, we  
3130 found history-congruence to be significantly autocorrelated for up to 21 trials (Figure 2B),  
3131 while controlling for task difficulty and the sequence of presented stimuli (Supplemental  
3132 Figure 2A-B).

- 3133 • Group-level autocorrelation curves in mice: At the group level, we found significant auto-  
3134 correlations in both stimulus-congruence (42 consecutive trials) and history-congruence  
3135 (8 consecutive trials (Figure 3B), while controlling for the respective autocorrelation of  
3136 task difficulty and external stimulation (Supplemental Figure 2C-D).
- 3137 • Correlation between stimulus- and history-congruence in humans: When perceptual  
3138 choices were less biased toward external information, participants relied more strongly  
3139 on internal information acquired from perceptual history (and vice versa,  $\beta = -0.05 \pm$   
3140  $5.63 \times 10^{-4}$ ,  $T(2.1 \times 10^6) = -84.21$ ,  $p < 2.2 \times 10^{-308}$ , **controlling for fluctuations in**  
3141 **general response biases**; Supplemental Section 9.2).
- 3142 • Correlation between stimulus- and history-congruence in mice: Fluctuations in the  
3143 strength of history-congruent biases had a significant effect on stimulus-congruence ( $\beta_1$   
3144  $= -0.12 \pm 7.17 \times 10^{-4}$ ,  $T(1.34 \times 10^6) = -168.39$ ,  $p < 2.2 \times 10^{-308}$ ) beyond the effect  
3145 of ongoing changes in general response biases ( $\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$ ,  $T(1.34 \times 10^6)$   
3146  $= -48.14$ ,  $p < 2.2 \times 10^{-308}$ ).

### 3147 10.3.8 Comment 8

3148 The central empirical finding is potentially important but is currently shadowed  
3149 by more speculative sections/ discussions. For instance, the section on the  
3150 adaptive merits of the computational model is relatively weaker compared to the  
3151 empirical results. In particular, the model is simulated without feedback (whereas  
3152 most experiments employ trial by trial feedback) and does not outperform the  
3153 baseline model in accuracy but in other secondary metrics.

3154 We agree with the Reviewer (see also a similar suggestion by Reviewer 1 in Comment 9).  
3155 We have removed the section 5.8 and the associated subsection of the discussion from our  
3156 manuscript. We will develop a model on the potential function of between-mode fluctuations  
3157 in a separate publication.

3158 **Minor comments:**

3159 **10.3.9 Comment 9**

3160 **The amount of statistical analysis and results is often overwhelming. The authors**  
3161 **could streamline the presentation better such that the main result is brought to**  
3162 **the foreground. Currently the manuscript resembles a technical report.**

3163 We apologize for this. From the Results, we have moved a number of sections to the  
3164 Supplemental Materials to stream-line the manuscript (i.e., our analysis of general response  
3165 biases [former section 5.4], the analysis of psychometric functions [former section 5.5], and  
3166 the respective paragraphs on the IBL database). From the Discussion, we have removed the  
3167 section on self-organized criticality (also following the suggestion of Reviewer 1). We have  
3168 also moved more peripheral statistical results to the figure legends and the method section:

3169 • We have moved the statistics on exponential decay in the autocorrelation to the figure  
3170 legends of Figure 2B and 3B.

3171 • We have shortened the description of logistic regression models that predict the stimulus-  
3172 and history-congruence at the index trial from the stimulus- and history-congruence at  
3173 the preceding trials.

3174 • The section on mouse behavior now matches the logic and presentation of results in the  
3175 human section.

3176 We hope that these changes will increase the readability of our manuscript.

3177 **10.3.10 Comment 10**

3178 **Some typos or omissions may alter the meaning in various places. Indicatively,**  
3179 **in lines 273, 439, 649.**

3180 Thanks a lot, we have corrected these typos.

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