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Bimodal Inference in Mice and Men

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¹ 2 Abstract

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

¹⁴ 3 One sentence summary

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

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¹⁸ **4 Introduction**

¹⁹ The capacity to respond to changes in the environment is a defining feature of life^{1–3}. In-
²⁰ triguingly, the ability of living things to process their surroundings fluctuates considerably
²¹ over time^{4,5}. In humans and mice, perception^{6–12}, cognition¹³ and memory¹⁴ cycle through
²² prolonged periods of enhanced and reduced sensitivity to external information, suggesting
²³ that the brain detaches from the world in recurring intervals that last from milliseconds
²⁴ to seconds and even minutes⁴. Yet breaking from external information is risky, as swift
²⁵ responses to the environment are often crucial to survival.

²⁶ What could be the reason for these fluctuations in perceptual performance¹¹? First, periodic
²⁷ fluctuations in the ability to parse external information^{11,15,16} may arise simply due to band-
²⁸ width limitations and noise. Second, it may be advantageous to actively reduce the costs
²⁹ of neural processing by seeking sensory information only in recurring intervals¹⁷, otherwise
³⁰ relying on random or stereotypical responses to the external world. Third, spending time
³¹ away from the ongoing stream of sensory inputs may also reflect a functional strategy that
³² facilitates flexible behavior and learning¹⁸: Intermittently relying more strongly on informa-
³³ tion acquired from past experiences may enable agents to build up stable internal predictions
³⁴ about the environment despite an ongoing stream of external sensory signals¹⁹. By the same
³⁵ token, recurring intervals of enhanced sensitivity to external information may help to detect
³⁶ changes in both the state of the environment and the amount of noise that is inherent in
³⁷ sensory encoding¹⁹.

³⁸ In this work, we sought to elucidate whether periodicities in the sensitivity to external infor-
³⁹ mation represent an epiphenomenon of limited processing capacity or, alternatively, result
⁴⁰ from a structured and adaptive mechanism of perceptual inference. To this end, we analyzed
⁴¹ two large-scale datasets on perceptual decision-making in humans²⁰ and mice²¹. **When less**
⁴² **sensitive to external stimulus information, humans and mice did not behave**
⁴³ **more randomly, but showed stronger serial dependencies in their perceptual**

⁴⁴ choices^{22–33}. These serial dependencies may be understood as driven by internal predictions that reflect the autocorrelation of natural environments³⁴ and bias perception toward preceding experiences^{30,31,35}. Computational modeling indicated that ongoing changes in perceptual performance may be driven by systematic fluctuations between externally- and internally-oriented *modes* of sensory analysis. **We suggest that such *bimodal inference* may help to build stable internal representations of the sensory environment despite an ongoing stream of sensory information.**

⁵¹ 5 Results

⁵² 5.1 Human perception fluctuates between epochs of enhanced and ⁵³ reduced sensitivity to external information

⁵⁴ We began by selecting 66 studies from the Confidence Database²⁰ that investigated how human participants ($N = 4317$) perform binary perceptual decisions (Figure 1A; see Methods for details on inclusion criteria). As a metric for perceptual performance (i.e., the sensitivity to external sensory information), we asked whether the participant’s response and the presented stimulus matched (*stimulus-congruent* choices) or differed from each other (*stimulus-incongruent* choices; Figure 1B and C) in a total of 21.05 million trials.

⁶⁰ In a first step, we asked whether the ability to accurately perceive sensory stimuli is constant over time or, alternatively, fluctuates in periods of enhanced and reduced sensitivity to external information. We found perception to be stimulus-congruent in $73.46\% \pm 0.15\%$ of trials (mean \pm standard error of the mean; Figure 2A), which was highly consistent across the selected studies (Supplemental Figure S1A). **In line with previous work⁸, we found that the probability of stimulus-congruence was not independent across successive trials: At the group level, stimulus-congruent perceptual choices were significantly autocorrelated for up to 15 trials (Figure 2B), controlling for task**

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

69 At the level of individual participants, the autocorrelation of stimulus-congruence exceeded
70 the respective autocorrelation of randomly permuted data within an interval of $3.24 \pm$
71 2.39×10^{-3} trials (Figure 2C). In other words, if a participant's experience was congru-
72 ent (or incongruent) with the external stimulus information at a given trial, her perception
73 was more likely to remain stimulus-congruent (or -incongruent) for approximately 3 trials
74 into the future. **The autocorrelation of stimulus-congruence was corroborated by**
75 **logistic regression models that successfully predicted the stimulus-congruence of**
76 **perception at the index trial $t = 0$ from the stimulus-congruence at the preceding**
77 **trials within a lag of 16 trials (Supplemental Figure S3).**

78 These results confirm that the ability to process sensory signals is not constant over time but
79 unfolds in multi-trial epochs of enhanced and reduced sensitivity to external information⁸.

80 As a consequence of this autocorrelation, the dynamic probability of stimulus-congruent
81 perception (i.e., computed in sliding windows of ± 5 trials; Figure 1C) fluctuated considerably
82 within participants (average minimum: $35.46\% \pm 0.22\%$, maximum: $98.27\% \pm 0.07\%$). In
83 line with previous findings⁹, such fluctuations in the sensitivity to external information had
84 a power density that was inversely proportional to the frequency in the slow spectrum¹¹
85 ($\text{power} \sim 1/f^\beta$, $\beta = -1.32 \pm 3.14 \times 10^{-3}$, $T(1.84 \times 10^5) = -419.48$, $p = 0$; Figure 2D).
86 This feature, which is also known as a **$1/f$ power law**^{36,37}, represents a characteristic of
87 scale-free fluctuations in complex dynamic systems such as the brain³⁸ and the cognitive
88 processes it entertains^{9,10,13,39,40}.

89 **5.2 Humans fluctuate between external and internal modes of sen-
90 sory processing**

91 In a second step, we sought to explain why perception cycles through periods of enhanced and
92 reduced sensitivity to external information⁴. We reasoned that observers may intermittently

93 rely more strongly on internal information, i.e., on predictions about the environment that
94 are constructed from previous experiences^{19,31}.

95 In perception, *serial dependencies* represent one of the most basic internal predictions that
96 cause perceptual decisions to be systematically biased toward preceding choices^{22–33}. Such
97 effects of perceptual history mirror the continuity of the external world, in which the recent
98 past often predicts the near future^{30,31,34,35,41}. Therefore, as a metric for the perceptual
99 impact of internal information, we computed whether the participant’s response at a given
100 trial matched or differed from her response at the preceding trial (*history-congruent* and
101 *history-incongruent perception*, respectively; Figure 1B and C).

102 First, we confirmed that perceptual history played a significant role in perception despite the
103 ongoing stream of external information. With a global average of $52.7\% \pm 0.12\%$ history-
104 congruent trials, we found a small but highly significant perceptual bias towards preced-
105 ing experiences ($\beta = 16.18 \pm 1.07$, $T(1.09 \times 10^3) = 15.07$, $p = 10^{-46}$; Figure 2A) that
106 was largely consistent across studies (Supplemental Figure 1B) and more pronounced in
107 participants who were less sensitive to external sensory information (Supplemental Figure
108 1C). Importantly, history-congruence was not a corollary of the sequence of presented stim-
109 uli: History-congruent perceptual choices were more frequent at trials when perception was
110 stimulus-incongruent ($56.03\% \pm 0.2\%$) as opposed to stimulus-congruent ($51.77\% \pm 0.11\%$,
111 $\beta = -4.26 \pm 0.21$, $T(8.57 \times 10^3) = -20.36$, $p = 5.28 \times 10^{-90}$; Figure 2A, lower panel).
112 Despite being adaptive in autocorrelated real-world environments^{19,34,35,42}, perceptual his-
113 tory thus represented a **source of bias** in the randomized experimental designs studied
114 here^{24,28,30,31,43}. These **serial biases were effects of choice history**, i.e., driven by
115 **the experiences reported at the preceding trial, and could not be attributed to**
116 **stimulus history**, i.e., to effects of the stimuli presented at the preceding trial
117 **(Supplemental Section 9.1)**.

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

119 tion is characterized by stronger or weaker biases toward preceding experiences. **In close**
120 **analogy to stimulus-congruence, we found history-congruence to be significantly**
121 **autocorrelated for up to 21 trials (Figure 2B), while controlling for task dif-**
122 **ficulty and the sequence of presented stimuli (Supplemental Figure 2A-B).** In
123 individual participants, the autocorrelation of history-congruence was elevated above ran-
124 domly permuted data for a lag of $4.87 \pm 3.36 \times 10^{-3}$ trials (Figure 2C), confirming that
125 the autocorrelation of history-congruence was not only a group-level phenomenon. The
126 autocorrelation of history-congruence was corroborated by logistic regression models that
127 successfully predicted the history-congruence of perception at an index trial $t = 0$ from the
128 history-congruence at the preceding trials within a lag of 17 trials (Supplemental Figure S3).

129 Third, we asked whether the impact of internal information fluctuates as **a scale-invariant**
130 **process with a 1/f power law (i.e., the feature typically associated with fluctua-**
131 **tions in the sensitivity to external information**^{9,10,13,39,40}). The dynamic probability
132 of history-congruent perception (i.e., computed in sliding windows of ± 5 trials; Figure 1C)
133 varied considerably over time, ranging between a minimum of $12.77\% \pm 0.14\%$ and a maxi-
134 mum $92.23\% \pm 0.14\%$. In analogy to stimulus-congruence, we found that history-congruence
135 fluctuated as at power densities that were inversely proportional to the frequency in the slow
136 spectrum¹¹ ($\text{power} \sim 1/f^\beta$, $\beta = -1.34 \pm 3.16 \times 10^{-3}$, $T(1.84 \times 10^5) = -423.91$, $p = 0$;
137 Figure 2D).

138 Finally, we ensured that fluctuations in stimulus- and history-congruence are linked to each
139 other. When perceptual choices were less biased toward external information, participants
140 relied more strongly on internal information acquired from perceptual history (and vice versa,
141 $\beta = -0.05 \pm 5.63 \times 10^{-4}$, $T(2.1 \times 10^6) = -84.21$, $p = 0$, **controlling for fluctuations in**
142 **general response biases**; Supplemental Section 9.2). Thus, while sharing the **1/f power**
143 **law** characteristic, fluctuations in stimulus- and history-congruence were shifted against each
144 other by approximately half a cycle and showed a squared coherence of $6.49 \pm 2.07 \times 10^{-3}\%$

¹⁴⁵ (Figure 2E and F; we report the average phase and coherence for frequencies below 0.1
¹⁴⁶ $1/N_{trials}$; see Methods for details).

¹⁴⁷ In sum, our analyses indicate that perceptual decisions may result from a competition be-
¹⁴⁸ tween external sensory signals with internal predictions provided by perceptual history. We
¹⁴⁹ show that the impact of these external and internal sources of information is not stable
¹⁵⁰ over time, but fluctuates systematically, emitting overlapping autocorrelation curves and
¹⁵¹ antiphase $1/f$ profiles.

¹⁵² These links between stimulus- and history-congruence suggest that the fluctuations in the
¹⁵³ impact of external and internal information may be generated by a unifying mechanism that
¹⁵⁴ causes perception to alternate between two opposing *modes*¹⁸ (Figure 1D): During *external*
¹⁵⁵ *mode*, perception is more strongly driven by the available external stimulus information.
¹⁵⁶ Conversely, during *internal mode*, participants rely more heavily on internal predictions
¹⁵⁷ that are implicitly provided by preceding perceptual experiences. The fluctuations in the
¹⁵⁸ degree of bias toward external versus internal information created by such *bimodal inference*
¹⁵⁹ may thus provide a novel explanation for ongoing fluctuations in the sensitivity to external
¹⁶⁰ information^{4,5,18}.

¹⁶¹ 5.3 Internal and external modes of processing facilitate re- ¹⁶² sponse behavior and enhance confidence in human perceptual ¹⁶³ decision-making

¹⁶⁴ The above results point to systematic fluctuations in the *decision variable*⁴⁴ that
¹⁶⁵ determines perceptual choices, causing enhanced sensitivity to external stimu-
¹⁶⁶ lus information during external mode and increased biases toward preceding
¹⁶⁷ choices during internal mode. As such, fluctuations in mode should influence
¹⁶⁸ downstream aspects of behavior and cognition that operate on the perceptual
¹⁶⁹ decision variable⁴⁴. To test this hypothesis with respect to motor behavior and

¹⁷⁰ metacognition, we asked how bimodal inference relates to response times (RTs)
¹⁷¹ and confidence reports.

¹⁷² With respect to RTs, we observed faster responses for stimulus-congruent as opposed to
¹⁷³ stimulus-incongruent choices ($\beta = -0.14 \pm 1.6 \times 10^{-3}$, $T(1.99 \times 10^6) = -85.84$, $p = 0$;
¹⁷⁴ Figure 2G). Intriguingly, whilst controlling for the effect of stimulus-congruence, we found
¹⁷⁵ that history-congruent (as opposed to history-incongruent) choices were also characterized
¹⁷⁶ by faster responses ($\beta = -9.56 \times 10^{-3} \pm 1.37 \times 10^{-3}$, $T(1.98 \times 10^6) = -6.97$, $p = 3.15 \times 10^{-12}$;
¹⁷⁷ Figure 2G).

¹⁷⁸ **When analyzing the speed of response against the mode of sensory processing (Figure 2H),
¹⁷⁹ we found that RTs were shorter during externally-oriented perception ($\beta_1 = -11.07 \pm 0.55$,
¹⁸⁰ $T(1.98 \times 10^6) = -20.14$, $p = 3.17 \times 10^{-90}$). Crucially, as indicated by a quadratic relationship
¹⁸¹ between the mode of sensory processing and RTs ($\beta_2 = -19.86 \pm 0.52$, $T(1.98 \times 10^6) =$
¹⁸² -38.43 , $p = 5 \times 10^{-323}$), participants became faster at indicating their perceptual decision
¹⁸³ when biases toward both internal and external mode grew stronger.

¹⁸⁴ In analogy to the speed of response, confidence was higher for stimulus-congruent as opposed
¹⁸⁵ to stimulus-incongruent choices ($\beta = 0.04 \pm 1.18 \times 10^{-3}$, $T(2.06 \times 10^6) = 36.85$, $p =$
¹⁸⁶ 3.25×10^{-297} ; Figure 2I). Yet whilst controlling for the effect of stimulus-congruence, we
¹⁸⁷ found that history-congruence also increased confidence ($\beta = 0.48 \pm 1.38 \times 10^{-3}$, $T(2.06 \times 10^6)$
¹⁸⁸ $= 351.54$, $p = 0$; Figure 2I).**

¹⁸⁹ When depicted against the mode of sensory processing (Figure 2J), subjective confidence was
¹⁹⁰ indeed enhanced when perception was more externally-oriented ($\beta_1 = 92.63 \pm 1$, $T(2.06 \times 10^6)$
¹⁹¹ $= 92.89$, $p = 0$). Importantly, however, participants were more confident in their perceptual
¹⁹² decision for stronger biases toward both internal and external mode ($\beta_2 = 39.3 \pm 0.94$,
¹⁹³ $T(2.06 \times 10^6) = 41.95$, $p = 0$). In analogy to RTs, subjective confidence thus showed a
¹⁹⁴ quadratic relationship to the mode of sensory processing (Figure 2J).

¹⁹⁵ Consequently, our findings predict that human participants lack full metacognitive insight

196 into how strongly external signals and internal predictions contribute to perceptual decision-
197 making. Stronger biases toward perceptual history thus lead to two seemingly contradictory
198 effects, more frequent errors (Supplemental Figure 1C) and increasing subjective confidence
199 (Figure 2I-J). This observation generates an intriguing prediction regarding the association of
200 between-mode fluctuations and perceptual metacognition: Metacognitive efficiency should
201 be lower in individuals who spend more time in internal mode, since their confidence re-
202 ports are less predictive of whether the corresponding perceptual decision is correct. We
203 computed each participant's M-ratio⁴⁵ ($\text{meta-d}'/\text{d}' = 0.85 \pm 0.02$) to probe this hypoth-
204 esis independently of inter-individual differences in perceptual performance. Indeed, we
205 found that biases toward internal information (as defined by the average probability of
206 history-congruence) were stronger in participants with lower metacognitive efficiency ($\beta =$
207 $-2.98 \times 10^{-3} \pm 9.82 \times 10^{-4}$, $T(4.14 \times 10^3) = -3.03$, $p = 2.43 \times 10^{-3}$).

208 In sum, the above results indicate that reporting behavior and metacognition do not map
209 linearly onto the mode of sensory processing. Rather, they suggest that slow fluctuations in
210 the respective impact of external and internal information are most likely to affect percep-
211 tion at an early level of sensory analysis^{46,47}. Such low-level processing may thus integrate
212 perceptual history with external inputs into a decision variable⁴⁴ that influences not only
213 perceptual choices, but also the speed and confidence at which they are made.

214 **In what follows, we probe alternative explanations for between-mode fluctua-**
215 **tions, test for the existence of modes in mice, and propose a predictive pro-**
216 **cessing model that explains fluctuations in mode ongoing shifts in the precision**
217 **afforded to external sensory information relative to internal predictions driven**
218 **by perceptual history.**

219 5.4 Fluctuations between internal and external mode cannot be
220 reduced to general response biases or random choices

221 The core assumption of bimodal inference - that ongoing changes in the sen-
222 sitivity to external information are driven by internal predictions induced via
223 perceptual history - needs to be contrasted against two alternative hypotheses:
224 When making errors, observers may not engage with the task and respond stereo-
225 typically, i.e., exhibit stronger general biases toward one of the two potential
226 outcomes, or simply choose randomly.

227 Logistic regression confirmed that perceptual history made a significant contri-
228 bution to perception ($\beta = 0.11 \pm 5.79 \times 10^{-3}$, $z = 18.53$, $p = 1.1 \times 10^{-76}$) over and
229 above the ongoing stream of external sensory information ($\beta = 2.2 \pm 5.87 \times 10^{-3}$,
230 $z = 375.11$, $p = 0$) and general response biases toward ($\beta = 15.19 \pm 0.08$, $z =$
231 184.98 , $p = 0$).

232 When eliminating perceptual history as a predictor of individual choices at indi-
233 vidual trials, Akaike Information Criterion (AIC⁴⁸) increased by $\delta_{AIC} = 1.64 \times 10^3$
234 (see Supplemental Figure S4A-B for parameter- and model-level inference at the
235 level of individual observers). Likewise, when eliminating slow fluctuations in
236 history-congruence as a predictor of slow fluctuations in stimulus-congruence
237 across trials, we observed an increase in AIC by $\delta_{AIC} + 7.06 \times 10^3$. These results
238 provided model-level evidence against the null hypotheses that fluctuations in
239 stimulus-congruence are driven exclusively by choice randomness or general re-
240 sponse bias (see Supplemental Section 9.2 and Supplemental Figure S5 for an
241 in-depth assessment of general response bias).

242 To confirm that changes in the sensitivity to external information are indicative
243 of internal mode processing, we estimated full and history-dependent psychome-
244 tric curves during internal, external, and across modes²¹. If, as we hypothesized,

internal mode processing reflects an enhanced impact of perceptual history, one would expect a history-dependent increase in biases and lapses as well as a history-independent increase in threshold. Conversely, if internal mode processing were driven by random choices, one would expect a history-independent increase in biases and threshold, and no change in bias. In line with our prediction, we found that internal mode processing was associated with a history-dependent increase in bias and lapse as well as a history-independent increase in threshold (Supplemental Section 9.3.1 and Supplemental Figure S6). This confirmed that internal mode processing is indeed driven by an enhanced impact of perceptual history.

In line with this, the quadratic relationship between mode and confidence (Figure 2J) suggested that biases toward internal information do not reflect a post-perceptual strategy of repeating preceding choices when the subjective confidence in the perceptual decision is low. Moreover, while responses became faster with increased exposure to the experiments of the Confidence database, the frequency of history-congruent choices increased over time, speaking against the proposition that participants stereotypically repeat preceding choices when not yet familiar with the experimental task (Supplemental Section 9.4.1).

Taken together, our results thus argue against recurring intervals of low task engagement, which may be signaled by stereotypical or random responses, as an alternative explanation for the phenomenon that we identify as bimodal inference.

267 **5.5 Mice fluctuate between external and internal modes of sensory
268 processing**

269 In a prominent functional explanation for serial dependencies^{22–28,32,33,46}, perceptual history
270 is cast as an internal prediction that leverages the temporal autocorrelation of natural en-
271 vironments for efficient decision-making^{30,31,34,35,41}. Since this autocorrelation is one of the
272 most basic features of our sensory world, fluctuating biases toward preceding perceptual
273 choices should not be a uniquely human phenomenon.

274 To test whether externally- and internally-oriented modes of processing exist beyond the
275 human mind, we analyzed data on perceptual decision-making in mice that were extracted
276 from the International Brain Laboratory (IBL) dataset²¹. We restricted our analyses to the
277 *basic task*²¹, in which mice responded to gratings of varying contrast that appeared either
278 in the left or right hemifield of with equal probability. We excluded sessions in which mice
279 did not respond correctly to stimuli presented at a contrast above 50% in more than 80% of
280 trials (see Methods for details), which yielded a final sample of N = 165 adequately trained
281 mice that went through 1.46 million trials.

282 We found perception to be stimulus-congruent in $81.37\% \pm 0.3\%$ of trials (Figure 3A, upper
283 panel). In line with humans, mice were biased toward perceptual history in $54.03\% \pm 0.17\%$
284 of trials ($T(164) = 23.65$, $p = 9.98 \times 10^{-55}$; Figure 3A and Supplemental Figure S1D). Since
285 the *basic task* of the IBL dataset presented stimuli at random in either the left or right
286 hemifield²¹, we expected stronger biases toward perceptual history to decrease perceptual
287 performance. Indeed, history-congruent choices were more frequent when perception was
288 stimulus-incongruent ($61.59\% \pm 0.07\%$) as opposed to stimulus-congruent ($51.81\% \pm 0.02\%$,
289 $T(164) = 31.37$, $p = 3.36 \times 10^{-71}$; $T(164) = 31.37$, $p = 3.36 \times 10^{-71}$; Figure 3A, lower panel),
290 confirming that perceptual history was a **source of bias**^{24,28,30,31,43} as opposed to a feature
291 of the experimental paradigm.

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

293 congruence (42 consecutive trials) and history-congruence (8 consecutive trials;
294 Figure 3B), while controlling for the respective autocorrelation of task difficulty
295 and external stimulation (Supplemental Figure 2C-D). In contrast to humans, mice
296 showed a negative autocorrelation coefficient of stimulus-congruence at trial 2, which was
297 due to a feature of the experimental design: Errors at a contrast above 50% were followed
298 by a high-contrast stimulus at the same location. Thus, stimulus-incongruent choices on
299 easy trials were more likely to be followed by stimulus-congruent perceptual choices that
300 were facilitated by high-contrast visual stimuli²¹.

301 At the level of individual mice, autocorrelation coefficients were elevated above randomly
302 permuted data within a lag of 4.59 ± 0.06 trials for stimulus-congruence and 2.58 ± 0.01 trials
303 for history-congruence (Figure 3C). **We corroborated these autocorrelations in logistic**
304 **regression models that successfully predicted the stimulus-/history-congruence**
305 **of perception at the index trial $t = 0$ from the stimulus-/history-congruence at**
306 **the 33 preceding trials for stimulus-congruence and 8 preceding trials for history-**
307 **congruence (Supplemental Figure S3)**. In analogy to humans, mice showed anti-phase
308 1/f fluctuations in the sensitivity to internal and external information (Figure 3D-F).

309 **The above results confirm that fluctuations between internally- and externally-**
310 **biased modes generalize to perceptual decision-making in mice. Following our**
311 **hypothesis that bimodal inference operates at the level of perception, we pre-**
312 **dicted that between-mode fluctuations modulate a decision variable⁴⁴ that de-**
313 **termines not only perceptual choices, but also downstream aspects of mouse**
314 **behavior⁴⁴**. We therefore asked how external and internal modes relate to the trial dura-
315 **tion (TD, a coarse measure of RT in mice that spans the interval from stimulus onset to**
316 **feedback²¹)**. Stimulus-congruent (as opposed to stimulus-incongruent) choices were associ-
317 **ated with shorter TDs ($\delta = -262.48 \pm 17.1$, $T(164) = -15.35$, $p = 1.55 \times 10^{-33}$), while**
318 **history-congruent choices were characterized by longer TDs ($\delta = 30.47 \pm 5.57$, $T(164) =$**

³¹⁹ 5.47, $p = 1.66 \times 10^{-7}$; Figure 3G).

³²⁰ Across the full spectrum of the available data, TDs showed a linear relationship with the
³²¹ mode of sensory processing, with shorter TDs during external mode ($\beta_1 = -4.16 \times 10^4 \pm$
³²² 1.29×10^3 , $T(1.35 \times 10^6) = -32.31$, $p = 6.03 \times 10^{-229}$, Figure 3H). However, an explorative
³²³ post-hoc analysis limited to TDs that differed from the median TD by no more than $1.5 \times$
³²⁴ MAD (median absolute distance⁴⁹) indicated that, when mice engaged with the task more
³²⁵ swiftly, TDs did indeed show a quadratic relationship with the mode of sensory processing
³²⁶ ($\beta_2 = -1.97 \times 10^3 \pm 843.74$, $T(1.19 \times 10^6) = -2.34$, $p = 0.02$, Figure 3I).

³²⁷ As in humans, it is important to ensure that ongoing changes in the sensitivity to external
³²⁸ information are indeed driven by perceptual history and cannot be reduced to general choice
³²⁹ biases or random behavior. Logistic regression confirmed a significant effect perceptual
³³⁰ history on perceptual choices ($\beta = 0.51 \pm 4.49 \times 10^{-3}$, $z = 112.84$, $p = 0$), while controlling
³³¹ for external sensory information ($\beta = 2.96 \pm 4.58 \times 10^{-3}$, $z = 646.1$, $p = 0$) and general
³³² response biases toward one of the two outcomes ($\beta = -1.78 \pm 0.02$, $z = -80.64$, $p = 0$).

³³³ **When eliminating perceptual history as a predictor of individual choices, AIC**
³³⁴ **increased by $\delta_{AIC} = 1.48 \times 10^4$, arguing against the notion that choice randomness**
³³⁵ **and general response bias are the only determinants of perceptual performance in**
³³⁶ **mice (see Supplemental Figure S4C-D for parameter- and model-level inference**
³³⁷ **in individual subjects).**

³³⁸ **In mice, fluctuations in the strength of history-congruent biases had a significant effect on
³³⁹ stimulus-congruence ($\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$, $p = 0$) beyond the
³⁴⁰ effect of ongoing changes in general response biases ($\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$, $T(1.34 \times 10^6)$
³⁴¹ $= -48.14$, $p = 0$). Eliminating the dynamic fluctuations in history-congruence as a predictor
³⁴² of fluctuations in stimulus-congruence resulted in an increase in AIC by $\Delta\{AIC\} + 2.8 \times 10^4$
³⁴³ (see Supplemental Section 9.2 and Supplemental Figure S5 for an in-depth assessment of
³⁴⁴ general response bias).**

345 When fitting full and history-conditioned psychometric curves to the IBL
346 data²¹, we observed that internal mode processing was associated with a
347 history-dependent increase in bias and lapse as well as a history-independent
348 increase in threshold (Supplemental Section 9.3.2 and Supplemental Figure
349 S7). Over time, the frequency of history-congruent choices increased alongside
350 stimulus-congruence and speed of response as mice were exposed to the exper-
351 iment, arguing against the proposition that biases toward perceptual history
352 reflected an unspecific response strategy in mice who were not sufficiently
353 trained on the IBL task (Supplemental Section 9.4.2 and Supplemental Figure
354 S8).

355 In sum, these analyses confirmed that the observed fluctuations in sensitivity
356 to external sensory information are driven by dynamic changes in impact of
357 perceptual history and cannot be reduced to general response bias and random
358 choice behavior.

359 5.6 Fluctuations in mode result from coordinated changes in the 360 impact of external and internal information on perception

361 The empirical data presented above indicate that, for both humans and mice, perception
362 fluctuates between external and modes, i.e., multi-trial epochs that are characterized by
363 enhanced sensitivity toward either external sensory information or internal predictions gen-
364 erated by perceptual history. Since natural environments typically show high temporal
365 redundancy³⁴, previous experiences are often good predictors of new stimuli^{30,31,35,41}. Se-
366 rial dependencies may therefore induce autocorrelations in perception by serving as internal
367 predictions (or *memory* processes^{9,13}) that actively integrate noisy sensory information over
368 time⁵⁰.

369 Previous work has shown that such internal predictions can be built by dynamically updat-

ing the estimated probability of being in a particular perceptual state from the sequence of preceding experiences^{35,46,51}. The integration of sequential inputs may lead to accumulating effects of perceptual history that progressively override incoming sensory information, enabling internal mode processing¹⁹. However, since such a process would lead to internal biases that may eventually become impossible to overcome⁵², **changes in mode may require** ongoing wave-like fluctuations^{9,13} in the perceptual impact of external and internal information that occur *irrespective* of the sequence of previous experiences and temporarily de-couple the decision variable from implicit internal representations of the environment¹⁹.

Following Bayes' theorem, binary perceptual decisions depend on the log posterior ratio L of the two alternative states of the environment that participants learn about via noisy sensory information⁵¹. We computed the posterior by combining the sensory evidence available at time-point t (i.e., the log likelihood ratio LLR) with the prior probability ψ , **weighted by the respective precision terms ω_{LLR} and ω_ψ** :

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

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

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

The LLR was computed from inputs s_t by applying a sigmoid function defined by parameter α that controls the sensitivity of perception to the available sensory information (see Methods for details on s_t in humans and mice):

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

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

390 To allow for bimodal inference, i.e., alternating periods of internally- and
 391 externally-biased modes of perceptual processing that occur irrespective of the
 392 sequence of preceding experiences, we assumed that likelihood and prior vary
 393 in their influence on the perceptual decision according to fluctuations governed
 394 by ω_{LLR} and ω_ψ . These anti-phase sine functions (defined by amplitudes $a_{LLR/\psi}$,
 395 frequency f and phase p) determine the precision afforded to the likelihood and
 396 prior⁵³. The implicit anti-phase fluctuations are mandated by Bayes-optimal
 397 formulations in which inference depends only on the relative values of prior and
 398 likelihood precision (i.e., the Kalman gain⁵⁴). As such, ω_{LLR} and ω_ψ implement
 399 a hyperprior⁵⁵ in which the likelihood and prior precisions are shifted against
 400 each other at a dominant timescale defined by f :

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

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

401 Finally, a sigmoid transform of the posterior L_t yields the probability of observing the
 402 perceptual decision y_t at a temperature determined by ζ^{-1} :

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

403 We used a maximum likelihood procedure to fit the bimodal inference model
404 (M1, Figure 1F) to the behavioral data from the Confidence database²⁰ and
405 the IBL database²¹, optimizing the parameters α , H , amp_{LLR} , amp_ψ , f and p (see
406 Methods for details and Supplemental Table T2 for a summary of the parameters
407 of the bimodal inference model). We validated our model in three steps:

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

415 Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model M3
416 ($AIC_3 = 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated only oscillations
417 of either likelihood or prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$ in humans
418 and 9.19×10^4 in mice) lacked any oscillations of likelihood and prior precision
419 and corresponded to the normative model proposed by Glaze et al.⁵¹. In model
420 M5 ($AIC_4 = 1.16 \times 10^5$ in humans and 1.14×10^5 in mice), we furthermore removed
421 the integration of information across trials, such that perception depended only
422 in incoming sensory information (Figure 1G).

423 The bimodal inference model achieved the lowest AIC across the full model space
424 ($AIC_1 = 4.73 \times 10^4$ in humans and 4.28×10^4 in mice) and was clearly superior to
425 the normative Bayesian model of evidence accumulation ($\delta_{AIC} = -5.08 \times 10^4$ in
426 humans and -4.91×10^4 in mice; Supplemental Figure S9).

427 As a second validation of the bimodal inference model, we tested whether the
428 posterior model predicted within-training and out-of-training variables. The

429 bimodal inference model characterizes each subject by a sensitivity parameter α
430 (humans: $\alpha = 0.5 \pm 1.12 \times 10^{-4}$; mice: $\alpha = 1.06 \pm 2.88 \times 10^{-3}$) that captures how
431 strongly perception is driven by the available sensory information, and a hazard
432 rate parameter H (humans: $H = 0.45 \pm 4.8 \times 10^{-5}$; mice: $H = 0.46 \pm 2.97 \times$
433 10^{-4}) that controls how heavily perception is biased by perceptual history. The
434 parameter f captures the dominant time scale at which likelihood (amplitude
435 humans: $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$; mice: $a_{LLR} = 0.39 \pm 1.08 \times 10^{-3}$) and prior
436 precision (amplitude humans: $a_\psi = 1.44 \pm 5.27 \times 10^{-4}$; mice: $a_\psi = 1.71 \pm 7.15 \times$
437 10^{-3}) fluctuated and was estimated at $0.11 \pm 1.68 \times 10^{-5}$ $1/N_{trials}$ and $0.11 \pm$
438 1.63×10^{-4} $1/N_{trials}$ in mice.

439 As a sanity check for model fit, we tested whether the frequency of stimulus- and history-
440 congruent trials in the Confidence database²⁰ and IBL database²¹ correlated with the es-
441 timated parameters α and H , respectively. As expected, the estimated sensitivity toward
442 stimulus information α was positively correlated with the frequency of stimulus-congruent
443 perceptual choices (humans: $\beta = 8.4 \pm 0.26$, $T(4.31 \times 10^3) = 32.87$, $p = 1.3 \times 10^{-211}$; mice:
444 $\beta = 1.93 \pm 0.12$, $T(2.07 \times 10^3) = 16.21$, $p = 9.37 \times 10^{-56}$). Likewise, H was negatively
445 correlated with the frequency of history-congruent perceptual choices (humans: $\beta = -11.84$
446 ± 0.5 , $T(4.29 \times 10^3) = -23.5$, $p = 5.16 \times 10^{-115}$; mice: $\beta = -6.18 \pm 0.66$, $T(2.08 \times 10^3) =$
447 -9.37 , $p = 1.85 \times 10^{-20}$).

448 Our behavioral analyses reveal that humans and mice show significant effects of percep-
449 tual history that impaired performance in randomized psychophysical experiments^{24,28,30,31,43}
450 (Figure 2A and 3A). We therefore expected that humans and mice underestimated the true
451 hazard rate \hat{H} of the experimental environments (Confidence database²⁰: $\hat{H}_{Humans} = 0.5$
452 $\pm 1.58 \times 10^{-5}$); IBL database²¹: $\hat{H}_{Mice} = 0.49 \pm 6.47 \times 10^{-5}$). Indeed, when fitting the
453 bimodal inference model to the trial-wise perceptual choices, we found that the estimated
454 (i.e., subjective) hazard rate H was lower than \hat{H} for both humans ($\beta = -6.87 \pm 0.94$,

₄₅₅ $T(61.87) = -7.33$, $p = 5.76 \times 10^{-10}$) and mice ($\beta = -2.91 \pm 0.34$, $T(112.57) = -8.51$, p
₄₅₆ $= 8.65 \times 10^{-14}$).

₄₅₇ To further probe the validity of the bimodal inference model, we asked whether posterior
₄₅₈ model quantities could explain aspects of the behavioral data that the model was not fitted
₄₅₉ to. We predicted that the posterior decision variable L_t not only encodes perceptual choices
₄₆₀ (i.e., the variable used for model estimation), but also predicts the speed of response and
₄₆₁ subjective confidence^{30,44}. Indeed, the estimated trial-wise posterior decision certainty $|L_t|$
₄₆₂ correlated negatively with RTs in humans ($\beta = -4.36 \times 10^{-3} \pm 4.64 \times 10^{-4}$, $T(1.98 \times 10^6)$
₄₆₃ $= -9.41$, $p = 5.19 \times 10^{-21}$) and TDs mice ($\beta = -35.45 \pm 0.86$, $T(1.28 \times 10^6) = -41.13$, p
₄₆₄ $= 0$). Likewise, subjective confidence reports were positively correlated with the estimated
₄₆₅ posterior decision certainty in humans ($\beta = 7.63 \times 10^{-3} \pm 8.32 \times 10^{-4}$, $T(2.06 \times 10^6) =$
₄₆₆ 9.18 , $p = 4.48 \times 10^{-20}$).

₄₆₇ **The dynamic accumulation of information inherent to our model entails that bi-**
₄₆₈ **ases toward perceptual history are stronger when the posterior decision certainty**
₄₆₉ **at the preceding trial is high**^{30,31,51}. Due to the link between posterior decision
₄₇₀ **certainty and confidence, confident perceptual choices should be more likely to**
₄₇₁ **induce history-congruent perception at the subsequent trial**^{30,31}. In line with our
₄₇₂ **prediction, logistic regression indicated that history-congruence was predicted**
₄₇₃ **by the posterior decision certainty $|L_{t-1}|$ extracted from the model** (humans: $\beta =$
₄₇₄ $8.22 \times 10^{-3} \pm 1.94 \times 10^{-3}$, $z = 4.25$, $p = 2.17 \times 10^{-5}$; mice: $\beta = -3.72 \times 10^{-3} \pm 1.83 \times 10^{-3}$,
₄₇₅ $z = -2.03$, $p = 0.04$) and the subjective confidence reported by the participants (humans:
₄₇₆ $\beta = 0.04 \pm 1.62 \times 10^{-3}$, $z = 27.21$, $p = 4.56 \times 10^{-163}$) at the preceding trial.

₄₇₇ **As a third validation of the bimodal inference model, we used the posterior**
₄₇₈ **model parameters to simulate synthetic perceptual choices and repeated the be-**
₄₇₉ **havioral analyses conducted for the empirical data.** Simulations from the bimodal
₄₈₀ inference model closely replicated our empirical results: Simulated perceptual decisions re-

481 sulted from a competition of perceptual history with incoming sensory signals (Figure 4A).
482 Stimulus- and history-congruence were significantly autocorrelated (Figure 4B-C), fluctuat-
483 ing in anti-phase as a scale-invariant process with a 1/f power law (Figure 4D-F). Simulated
484 posterior certainty^{28,30,44} (i.e., the absolute of the log posterior ratio $|L_t|$) showed a quadratic
485 relationship to the mode of sensory processing (Figure 4H), mirroring the relation of RTs
486 and confidence reports to external and internal biases in perception (Figure 2G-H and Fig-
487 ure 3G-H). Crucially, the overlap between empirical and simulated data broke down when
488 we removed the anti-phase oscillations or the accumulation of evidence over time from the
489 bimodal inference model (Supplemental Figures S10-13).

490 **In sum, computational modeling suggested that between-mode fluctuations are**
491 **best explained by two interlinked processes (Figure 1E and F): (i), the dynamic**
492 **accumulation of information across successive trials mandated by normative**
493 **Bayesian models of evidence accumulation and, (ii), ongoing anti-phase oscil-**
494 **lations in the impact of external and internal information.**

495 6 Discussion

496 This work investigates the behavioral and computational characteristics of ongoing fluctua-
497 tions in perceptual decision-making using two large-scale datasets in humans²⁰ and mice²¹.
498 We found that humans and mice cycle through recurring intervals of reduced sensitivity to
499 external sensory information, during which they rely more strongly on perceptual history,
500 i.e., an internal prediction that is provided by the sequence of preceding choices. Compu-
501 tational modeling indicated that these slow periodicities are governed by two interlinked
502 factors: (i), the dynamic integration of sensory inputs over time and, (ii), anti-phase os-
503 cillations in the strength at which perception is driven by internal versus external sources
504 of information. These cross-species results suggest that ongoing fluctuations in perceptual
505 decision-making arise not merely as a noise-related epiphenomenon of limited processing

506 capacity, but result from a structured and adaptive mechanism that fluctuates between
507 internally- and externally-oriented modes of sensory analysis.

508 **6.1 Bimodal inference represents a pervasive aspect of perceptual
509 decision-making in humans and mice**

510 A growing body of literature has highlighted that perception is modulated by preceding
511 choices^{22–28,30,32,33}. Our work provides converging cross-species evidence supporting the no-
512 tion that such serial dependencies are a pervasive and general phenomenon of perceptual
513 decision-making (Figures 2 and 3). While introducing errors in randomized psychophys-
514 ical designs^{24,28,30,31,43} (Figures 2A and 3A), we found that perceptual history facilitates
515 post-perceptual processes such as speed of response⁴² (Figure 2G and 3G) and subjective
516 confidence in humans (Figure 2I).

517 At the level of individual traits, increased biases toward preceding choices were associated
518 with reduced sensitivity to external information (Supplemental Figure 1C-D) and lower
519 metacognitive efficiency. When investigating how serial dependencies evolve over time, we
520 observed dynamic changes in the strength of perceptual history (Figures 2 and 3B) that
521 created wavering biases toward internally- and externally-biased modes of sensory process-
522 ing. Between-mode fluctuations may thus provide a new explanation for ongoing changes in
523 perceptual performance^{6–11}.

524 In computational terms, serial dependencies may leverage the temporal autocorrelation of
525 natural environments^{31,46} to increase the efficiency of decision-making^{35,43}. Such temporal
526 smoothing⁴⁶ of sensory inputs may be achieved by updating dynamic predictions about the
527 world based on the sequence of noisy perceptual experiences^{22,31}, **using algorithms based**
528 **on sequential Bayes^{25,42,51} such as Kalman³⁵ or Hierarchical Gaussian filtering⁵⁴.**
529 At the level of neural mechanisms, the integration of internal with external information may
530 be realized by combining feedback from higher levels in the cortical hierarchy with incoming

531 sensory signals that are fed forward from lower levels⁵⁶.

532 Yet relying too strongly on serial dependencies may come at a cost: When accumulating over
533 time, internal predictions may eventually override external information, leading to circular
534 and false inferences about the state of the environment⁵⁷. Akin to the wake-sleep-algorithm
535 in machine learning⁵⁸, bimodal inference may help to determine whether errors result from
536 external input or from internally-stored predictions: During internal mode, sensory pro-
537 cessing is more strongly constrained by predictive processes that auto-encode the agent's
538 environment. Conversely, during external mode, the network is driven predominantly by
539 sensory inputs¹⁸. Between-mode fluctuations may thus generate an unambiguous error sig-
540 nal that aligns internal predictions with the current state of the environment in iterative
541 test-update-cycles⁵⁸. On a broader scale, between-mode fluctuations may thus regulate the
542 balance between feedforward versus feedback contributions to perception and thereby play
543 a adaptive role in metacognition and reality monitoring⁵⁹.

544 **From the perspective of the Bayesian brain hypothesis, we hypothesized that**
545 **observers have certain hyperpriors that are apt for accommodating fluctuations**
546 **in the predictability of their environment, i.e., people believe that their world**
547 **is inherently volatile. To be Bayes optimal, it is therefore necessary to periodi-**
548 **cally re-evaluate posterior beliefs about the parameters that define an internal**
549 **generative model of the external sensory environment. One way to do this is**
550 **to periodically suspend the precision of prior beliefs and increase the precision**
551 **afforded to sensory evidence, thus updating Bayesian beliefs about model pa-**
552 **rameters.**

553 **The empirical evidence above suggests that the timescale of this periodic schedul-**
554 **ing of evidence accumulation may be scale-invariant. This means that there may**
555 **exist a timescale of periodic fluctuations in precision over every window or length**
556 **of perceptual decision-making. Bimodal inference predicts perceptual decisions**

557 under a generative model (based upon a hazard function to model serial depen-
558 dencies between subsequent trials) with periodic fluctuations in the precision of
559 sensory evidence relative to prior beliefs at a particular timescale. Remarkably,
560 a systematic model comparison based on AIC indicated that a model with fluc-
561 tuating precisions has much greater evidence, relative to a model in the absence
562 of fluctuating precisions. This ad-hoc addition of oscillations to a normative
563 Bayesian model of evidence accumulation⁵¹ allowed us to quantify the domi-
564 nant timescale of periodic fluctuations mode at approximately $0.11\ 1/N_{trials}$ in
565 humans and mice that is appropriate for these kinds of paradigms.

566 **6.2 Bimodal inference versus normative Bayesian evidence accu-**
567 **mulation**

568 Could bimodal inference emerge spontaneously in normative models of percep-
569 tual decision-making? In predictive processing, the relative precision of prior
570 and likelihood determines their integration into the posterior that determines
571 the content of perception. At the level of individual trials, the perceptual im-
572 pact of internal predictions generated from perceptual history (prior precision)
573 and external sensory information (likelihood precision) are thus necessarily anti-
574 correlated. The same holds for mechanistic models of drift diffusion, which
575 understand choice history biases as driven by changes in the starting point⁵¹ or
576 the drift rate of evidence accumulation³². Under the former formulation, per-
577 ceptual history is bound to have a stronger influence on perception when less
578 weight is given to incoming sensory evidence, assuming that the last choice is
579 represented as a starting point bias. The effects of choice history in normative
580 Bayesian and mechanistic drift diffusion models can be mapped onto one another
581 via the Bayesian formulation of drift diffusion⁶⁰, where the inverse of likelihood
582 precision determines the amount of noise in the accumulation of new evidence,

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

584 While it is thus clear that the impact of perceptual history and sensory evi-
585 dence are anti-correlated *at each individual trial*, we here introduce anti-phase
586 oscillations as an ad-hoc modification to model slow fluctuations in prior and
587 likelihood precision that evolve *over many consecutive trials* and are not man-
588 dated by normative Bayesian or mechanistic drift diffusion models. The bimodal
589 inference model provides a reasonable explanation of the linked autocorrelations
590 in stimulus- and history-congruence, as evidenced by formal model comparison,
591 successful prediction of RTs and confidence as out-of-training variables, and a
592 qualitative reproduction of our empirical data from posterior model parameter
593 as evidence against over- or under-fitting.

594 Of note, similar non-stationarities have been observed in descriptive models that
595 assume continuous⁶¹ or discrete¹² changes in the latent states that modulate per-
596 ceptual decision-making at slow timescales. A recent computational study⁶² has used
597 a Hidden Markov model to investigate perceptual decision-making in the IBL database²¹. In
598 analogy to our findings, the authors observed that mice switch between temporally extended
599 *strategies* that last for more than 100 trials: During *engaged* states, perception was highly
600 sensitive to external sensory information. During *disengaged* states, in turn, choice behavior
601 was prone to errors due to enhanced biases toward one of the two perceptual outcomes⁶².
602 Despite the conceptual differences to our approach (discrete states in a Hidden Markov
603 model that correspond to switches between distinct decision-making strategies⁶² vs. gradual
604 changes in mode that emerge from sequential Bayesian inference and ongoing **oscillations**
605 in the impact of external relative to internal information), it is tempting to speculate that en-
606 gaged/disengaged states and between-mode fluctuations might tap into the same underlying
607 phenomenon.

608 **6.3 Task engagement and residual motor activation as alternative
609 explanations for bimodal inference**

610 As a functional explanation for bimodal inference, we propose that perception
611 temporarily disengages from internal predictions to form stable inferences about
612 the statistical properties of the sensory environment. Between-mode fluctuations
613 may thus elude circular inferences that occur when both the causes and the
614 encoding of sensory stimuli are volatile^{19,57}. By the same token, we suggest that
615 fluctuations in mode occur at the level of perceptual processing^{26,30,46,47}, and are not a
616 passive phenomenon that is primarily driven by factors situated up- or downstream of sensory
617 analysis.

618 How does attention relate to phenomenon of between-mode fluctuations? Ac-
619 cording to predictive processing, attention corresponds to the precision afforded
620 to the probability distributions that underlie perceptual inference⁵³. From this
621 perspective, fluctuations between external and internal mode can be understood
622 as ongoing shifts in the attention afforded to either external sensory informa-
623 tion (regulated via likelihood precision) or internal predictions (regulated via
624 precision precision). When the precision of either likelihood or prior increases,
625 posterior precision increases, which leads to faster RTs and higher confidence.
626 Therefore, when defined from the perspective of predictive processing as the
627 precision afforded to likelihood and prior⁵³, fluctuations in attention may pro-
628 vide a plausible explanation for the quadratic relationship of mode to RTs and
629 confidence (Figure 2H and J; Figure 3I, Figure 4I).

630 Outside of the predictive processing field, attention is often understood in the
631 context of task engagement⁶³, which varies according to the availability of cog-
632 nitive resources that are modulated by factors such as tonic arousal, familiarity
633 with the task, or fatigue⁶³. Our results suggest that internal mode processing

634 cannot be completely reduced to intervals of low task engagement: In addition
635 to shorter RTs and elevated confidence, choices during internal mode were not
636 random or globally biased, but driven by perceptual history (Supplemental Sec-
637 tion). Moreover, our computational model identified the dominant timescale
638 of between-mode fluctuations at $0.11\sqrt{1/N_{trials}}$, which may be compatible with
639 fluctuations in arousal⁶⁴, but is faster than to be expected for the development
640 of task familiarity or fatigue.

641 However, in interpreting the impact of between-mode fluctuations on perceptual
642 accuracy, speed of response and confidence, it is important to consider that global
643 modulators such as tonic arousal are known to have non-linear effects on task
644 performance⁶⁵: In perceptual tasks, performance seems to be highest during
645 mid-level arousal, whereas low- and high-level arousal lead to reduced accuracy
646 and slower responses⁶⁵. This contrasts with the effects of bimodal inference,
647 where accuracy increases linearly as one moves from internal to external mode,
648 and responses become faster at both ends of the mode spectrum.

649 Of note, high phasic arousal has been shown to suppress biases in decision-
650 making in humans and mice across domains^{66–68}, including biases toward percep-
651 tual history²⁸ that we implicate in internal mode processing. While the increase
652 in response speed and history congruence over time (Supplemental Section 9.4)
653 may argue against insufficient training as an alternative explanation for inter-
654 internal mode processing, it may also be indicative of waning arousal. The multiple
655 mechanistic mappings to RTs and confidence warrant more direct measures of
656 arousal (such as pupil size^{28,65,66,68–70}, motor behavior^{69,70}, or neural data⁷¹) to
657 better delineate bimodal inference from fluctuations in global modulators of task
658 performance.

659 Residual activation of the motor system may provide another contribution to

660 serial biases in perceptual choices⁷². Such motor-driven priming may lead to
661 errors in randomized psychophysical designs, resembling the phenomenon that
662 we identify as internally-biased processing⁷³. Moreover, residual activation of the
663 motor system may lead to faster responses, and thus constitutes an alternative
664 explanation for the quadratic relationship of mode with RTs⁷². The observation
665 of elevated confidence for stronger biases toward internal mode speaks against
666 the proposition that residual activation of the motor system is the primary driver
667 of serial choice biases, since strong motor-driven priming should lead to frequent
668 lapses that are typically associated reduced confidence⁷⁴. Likewise, perceptual
669 history effects have repeatedly been replicated in experiments with counter-
670 balanced stimulus-response mappings^{30: Feigin2021}.

671 No-response paradigms, in which perceptual decision are inferred from eye-
672 movements alone, could help to better differentiate perceptual from motor-
673 related effects. Likewise, video-tracking of response behavior and neural record-
674 ing from motor- and premotor, which has recently been released for the IBL
675 database[IBL2023], may provide further insight into the relation of motor be-
676 havior to the perceptual phenomenon of between-mode fluctuations.

677 6.4 Limitations and open questions

678 Our results suggest bimodal inference as a pervasive aspect in perceptual
679 decision-making in humans and mice. However, a number of limitations and
680 open questions have to be considered:

681 First, this work sought to understand whether fluctuations between internal and
682 external mode, which we initially observed in an experiment on bistable percep-
683 tion in humans¹⁹, are general phenomenon that occurs across a diverse set of per-
684 ceptual decision-making tasks. Our analysis of the Confidence database²⁰ there-

685 fore collapsed across all available experiments on binary perceptual decision-
686 making. Individual experiments differed with respect to the stimuli, the manip-
687 ulation of difficulty, the timing of trials, and the way responses were collected,
688 but were highly comparable with respect to the central variables of stimulus-
689 and history-congruence (Supplemental Figure S1A-B).

690 The variability across experiments, which we considered as random effects in all
691 statistical analyses, enabled us to assess whether bimodal inference represents a
692 general phenomenon in perceptual decision-making, but limited the precision at
693 which we were able to investigate the relation of mode to behavioral variables
694 such as timing, task difficulty, RT or confidence. This issue is partially resolved
695 by our analyses of the IBL database, which replicated our findings in an exper-
696 iment that was highly standardized with respect to timing, task difficulty, and
697 behavioral read-out²¹. It will be an important task for future research to vali-
698 date our results on bimodal inference in a standardized dataset of comparable
699 volume in humans, which is, to our knowledge, not yet available.

700 Second, our results point to an attraction of perception toward preceding choices.
701 Previous work has shown that perceptual decision-making is concurrently af-
702 fected by both attractive and repulsive serial biases that operate on distinct time-
703 scales and serve complementary functions for sensory processing^{27,75,76}: Short-
704 term attraction may serve the decoding of noisy sensory inputs and increase
705 the stability of perception, whereas long-term repulsion may enable efficient en-
706 coding and sensitivity to change²⁷. In the data analyzed here, history biases
707 tended to be repetitive (Figure 2A, Figure 3A, Supplemental Figure S6 and S7),
708 as only 2 of the 66 experiments of the Confidence database²⁰ showed significant
709 alternating biases (Supplemental Figure S1). However, as we show in Supple-
710 mental Figure S14, fluctuations in both alternating and repeating history biases

711 generate overlapping autocorrelation curves. Our analysis of between-mode fluc-
712 tuations is therefore not tied exclusively to repeating biases, but accommodates
713 alternating biases as well, such that both may lead to internally-biased process-
714 ing and reduced sensitivity to external sensory information. Future work could
715 apply our approach to paradigms that boost alternating as opposed to repeating
716 biases, as this would help to better understand how repetition and alternation
717 are linked in terms of their computational function and neural implementation²⁷.

718 A third open question concerns the computational underpinnings of bimodal in-
719 ference. The addition of slow anti-phase oscillations to the integration of prior
720 and likelihood represents an ad-hoc modification of a normative Bayesian model
721 of evidence accumulation⁵¹. While the bimodal inference model is supported
722 by formal model comparison, the successful prediction of out-of-training vari-
723 ables and the qualitative reproduction of our empirical data in simulations from
724 posterior model parameters, it is an important task for future research to test
725 whether between-mode fluctuations can emerge spontaneously in hierarchical
726 models of Bayesian inference, whether modes are continuous¹⁹ or discrete⁶², and
727 whether bimodal inference can be causally manipulated by experimental vari-
728 ables. We speculate that between-mode fluctuations may separate the perceptual
729 contribution of internal predictions and external sensory data in time, creating
730 unambiguous learning signals that benefit inference about the precision of prior
731 and likelihood, respectively. This proposition should be tested empirically by
732 relating the phenomenon of bimodal inference to performance in, e.g., reversal
733 learning, probabilistic reasoning, or metacognition.

734 A final important avenue for further research on bimodal inference is identify-
735 ing the neurobiological underpinnings of bimodal inference. Since between-mode
736 fluctuations were found in humans and mice, future studies can apply non-invasive and inva-

737 sive neuro-imaging and electrophysiology to better understand the neural mechanisms that
738 generate ongoing changes in mode in terms of their neuro-anatomy, -chemistry and -circuitry.

739 Establishing the neural correlates of externally- an internally-biased modes will enable ex-
740 iting opportunities to investigate their role for adaptive perception and decision-making:
741 Causal interventions via pharmacological challenges, optogenetic manipulations or (non-
742)invasive brain stimulation will help to understand whether between-mode fluctuations are
743 implicated in resolving credit-assignment problems^{18,77} or in calibrating metacognition and
744 reality monitoring⁵⁹. Answers to these questions may provide new insights into the patho-
745 physiology of hallucinations and delusions, which have been characterized by an imbalance
746 in the impact of external versus internal information^{56,78,79} and are typically associated with
747 metacognitive failures and a departure from consensual reality⁷⁹.

⁷⁴⁸ **7 Methods**

⁷⁴⁹ **7.1 Resource availability**

⁷⁵⁰ **7.1.1 Lead contact**

⁷⁵¹ Further information and requests for resources should be directed to and will be fulfilled by
⁷⁵² the lead contact, Veith Weilnhammer (veith.weilnhammer@gmail.com).

⁷⁵³ **7.1.2 Materials availability**

⁷⁵⁴ This study did not generate new unique reagents.

⁷⁵⁵ **7.1.3 Data and code availability**

⁷⁵⁶ All custom code and behavioral data are available on <https://github.com/veithweilnhamer/Modes>. This manuscript was created using the *R Markdown* framework, which
⁷⁵⁷ integrates all data-related computations and the formatted text within one document. With
⁷⁵⁸ this, we wish to make our approach fully transparent and reproducible for reviewers and
⁷⁵⁹ future readers.

⁷⁶¹ **7.2 Experimental model and subject details**

⁷⁶² **7.2.1 Confidence database**

⁷⁶³ We downloaded the human data from the Confidence database²⁰ on 10/21/2020,
⁷⁶⁴ limiting our analyses to the category *perception*. Within this category, we se-
⁷⁶⁵ lected studies in which participants made binary perceptual decisions between
⁷⁶⁶ two alternatives. We excluded two experiments in which the average percep-
⁷⁶⁷ tual accuracy fell below 50%. After excluding these experiments, our sample
⁷⁶⁸ consisted of 21.05 million trials obtained from 4317 human participants and 66
⁷⁶⁹ individual experiments (Supplemental Table 1). Out of the 66 included exper-

770 iments, 62 investigated visual, 1 auditory, 2 proprioceptive, and 1 multimodal
771 perception. 59 experiments were based on discrimination and 6 on detection,
772 with one investigating both.

773 **7.2.2 IBL database**

774 We downloaded the data from the IBL database²¹ on 04/28/2021. We limited our analyses to
775 the *basic task*, during which mice responded to gratings that appeared with equal probability
776 in the left or right hemifield. Within each mouse, we excluded sessions in which perceptual
777 accuracy was below 80% for stimuli presented at a contrast $\geq 50\%$. After exclusion, our
778 sample consisted of 1.46 million trials obtained from N = 165 mice.

779 **7.3 Method details**

780 **7.3.1 Variables of interest**

781 **Primary variables of interest:** We extracted trial-wise data on the presented stimulus and
782 the associated perceptual decision. Stimulus-congruent choices were defined by perceptual
783 decisions that matched the presented stimuli. History-congruent choices were defined by
784 perceptual choices that matched the perceptual choice at the immediately preceding trial.
785 The dynamic probabilities of stimulus- and history-congruence were computed in sliding
786 windows of ± 5 trials.

787 The *mode* of sensory processing was derived by subtracting the dynamic probability of history-
788 congruence from the dynamic probability of stimulus-congruence, such that positive values
789 indicate externally-oriented processing, whereas negative values indicate internally-oriented
790 processing. When visualizing the relation of the mode of sensory processing to confidence,
791 RTs or trial duration (see below), we binned the mode variable in 10% intervals. We excluded
792 bins that contained less than 0.5% of the total number of available data-points.

793 **Secondary variables of interest:** From the Confidence Database²⁰, we furthermore ex-

794 tracted trial-wise confidence reports and RTs. **Out of the 58 experiments that provide**
795 **information on RTs, 46 cued the response by the onset of a response screen or**
796 **an additional response cue, whereas 14 allowed participants to response at any**
797 **time after stimulus onset.** If RTs were available for both the perceptual decision and
798 the confidence report, we only extracted the RT associated with the perceptual decision.
799 To enable comparability between studies, we normalized RTs and confidence reports within
800 individual studies using the *scale* R function. If not available for a particular study, RTs
801 were treated as missing variables. From the IBL database²¹, we extracted trial durations
802 (TDs) as defined by interval between stimulus onset and feedback, which represents a coarse
803 measure of RT²¹.

804 **Exclusion criteria for individual data-points:** For non-normalized data (TDs from the
805 IBL database²¹; d-prime, meta-dprime and M-ratio from the Confidence database²⁰ and
806 simulated confidence reports), we excluded data-points that differed from the median by
807 more than 3 x MAD (median absolute distance⁴⁹). For normalized data (RTs and confidence
808 reports from the Confidence database²⁰), we excluded data-points that differed from the
809 mean by more than 3 x SD (standard deviation).

810 7.3.2 Control variables

811 Next to the sequence of presented stimuli, we assessed the autocorrelation of task difficulty
812 as an alternative explanation for any autocorrelation in stimulus- and history-congruence. In
813 the Confidence Database²⁰, **21 of the 66 included experiments used fixed difficulty**
814 **levels, whereas 45 manipulated difficulty levels within participants.** Difficulty
815 **was manipulated via noise masks, contrast, luminance, presentation time, or**
816 **stimulus probability for gabors, dot coherence for random dot kinematograms,**
817 **difference in elements and set size for comparisons of numerosity, difference in**
818 **clicks for auditory discrimination, temporal distance for meta-contrast masking,**
819 **and amount of self-motion for proprioception.** We treated task difficulty as

820 **a missing variable for the experiments that fixed it at the participant-level,**
821 **as this precluded the computation of autocorrelation curves.** In analogy to RTs
822 and confidence, difficulty levels were normalized within individual studies. For the IBL
823 Database²¹, task difficulty was defined by the contrast of the presented grating.

824 **7.3.3 Autocorrelations**

825 For each participant, trial-wise autocorrelation coefficients were estimated using the R-
826 function *acf* with a maximum lag defined by the number of trials available per subject.
827 Autocorrelation coefficients are displayed against the lag (in numbers of trials, ranging from
828 1 to 20) relative to the index trial ($t = 0$; Figure 2B-C, 3B-C and 4B-C). To account for spu-
829 rious autocorrelations that occur due to imbalances in the analyzed variables, we estimated
830 autocorrelations for randomly permuted data (100 iterations). For group-level autocorrela-
831 tions, we computed the differences between the true autocorrelation coefficients and the mean
832 autocorrelation observed for randomly permuted data and averaged across participants.

833 At a given trial, group-level autocorrelation coefficients were considered significant when
834 linear mixed effects modeling indicated that the difference between real and permuted au-
835 tocorrelation coefficients was above zero at an alpha level of 0.05%. To test whether the
836 autocorrelation of stimulus- and history-congruence remained significant when controlling
837 for task difficulty and the sequence of presented stimuli, we added the respective autocorre-
838 lation as an additional factor to the linear mixed effects model that computed the group-level
839 statistics (see also *Mixed effects modeling*).

840 To assess autocorrelations at the level of individual participants, we counted the number of
841 subsequent trials (starting at the first trial after the index trial) for which less than 50% of
842 the permuted autocorrelation coefficients exceeded the true autocorrelation coefficient. For
843 example, a count of zero indicates that the true autocorrelation coefficients exceeded *less*
844 *than 50%* of the autocorrelation coefficients computed for randomly permuted data at the
845 first trial following the index trial. A count of five indicates that, for the first five trials

846 following the index trial, the true autocorrelation coefficients exceeded *more than 50%* of
847 the respective autocorrelation coefficients for the randomly permuted data; at the 6th trial
848 following the index trial, however, *less than 50%* of the autocorrelation coefficients exceeded
849 the respective permuted autocorrelation coefficients.

850 **7.3.4 Spectral analysis**

851 We used the R function *spectrum* to compute the spectral densities for the dynamic proba-
852 bilities of stimulus- and history-congruence as well as the phase (i.e., frequency-specific shift
853 between the two time-series ranging from 0 to $2*\pi$) and squared coherence (frequency-specific
854 variable that denotes the degree to which the shift between the two time-series is constant,
855 ranging from 0 to 100%). Periodograms were smoothed using modified Daniell smoothers at
856 a width of 50.

857 Since the dynamic probabilities of history- and stimulus-congruence were computed using
858 a sliding windows of ± 5 trials (i.e., intervals containing a total of 11 trials), we report the
859 spectral density, coherence and phase for frequencies below $1/11 \ 1/N_{trials}$. Spectral densities
860 have one value per subject and frequency (data shown in Figures 2D and 3D). To assess the
861 relation between stimulus- and history-congruence in this frequency range, we report average
862 phase and average squared coherence for all frequencies below $1/11 \ 1/N_{trials}$ (i.e., one value
863 per subject; data shown in Figure 2E-F and 3E-F).

864 Since the data extracted from the Confidence Database²⁰ consist of a large set of individual
865 studies that differ with respect to inter-trial intervals, we defined the variable *frequency* in the
866 dimension of cycles per trial $1/N_{trials}$ rather than cycles per second (Hz). For consistency,
867 we chose $1/N_{trials}$ as the unit of frequency for the IBL database²¹ as well.

868 **7.4 Quantification and statistical procedures**

869 All aggregate data are reported and displayed with errorbars as mean \pm standard error of
870 the mean.

871 **7.4.1 Mixed effects modeling**

872 Unless indicated otherwise, we performed group-level inference using the R-packages *lmer*
873 and *afer* for linear mixed effects modeling and *glmer* with a binomial link-function for logistic
874 regression. We compared models based on AIC. To account for variability between the studies
875 available from the Confidence Database²⁰, mixed modeling was conducted using random
876 intercepts defined for each study. To account for variability across experimental session
877 within the IBL database²¹, mixed modeling was conducted using random intercepts defined
878 for each individual session. When multiple within-participant datapoints were analyzed, we
879 estimated random intercepts for each participant that were *nested* within the respective study
880 of the Confidence database²⁰. By analogy, for the IBL database²¹, we estimated random
881 intercepts for each session that were nested within the respective mouse. We report β values
882 referring to the estimates provided by mixed effects modeling, followed by the respective T
883 statistic (linear models) or z statistic (logistic models).

884 The effects of stimulus- and history-congruence on RTs and confidence reports (Figure 2,
885 3 and 4, subpanels G-I) were assessed in linear mixed effects models that tested for main
886 effects of both stimulus- and history-congruence as well as the between-factor interaction.
887 Thus, the significance of any effect of history-congruence on RTs and confidence reports was
888 assessed while controlling for the respective effect of stimulus-congruence (and vice versa).

889 **7.4.2 Psychometric function**

890 We obtained psychometric curves by fitting the following error function to the behavioral
891 data:

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

892 We used the Broyden–Fletcher–Goldfarb–Shanno algorithm in maximum likelihood
 893 estimation⁸⁰ to predict individual choices y (outcome A: $y = 0$; outcome B: $y = 1$) from the
 894 choice probability y_p . In humans, we computed s_w by multiplying the inputs s (stimulus A:
 895 0; outcome B: 1) with the task difficulty D_b (binarized across 7 levels):

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

896 In mice, s_w was defined by the respective stimulus contrast in the two hemifields:

$$s_w = \text{Contrast}_{Right} - \text{Contrast}_{Left} \quad (10)$$

897 Parameters of the psychometric error function were fitted using the R-package *optimx*⁸⁰. The
 898 psychometric error function was defined via the parameters γ (lower lapse; lower bound =
 899 0, upper bound = 0.5), δ (upper lapse; lower bound = 0, upper bound = 0.5), μ (bias; lower
 900 bound humans = -5; upper bound humans = 5, lower bound mice = -0.5, upper bound mice
 901 = 0.5) and threshold t (lower bound humans = 0.5, upper bound humans = 25; lower bound
 902 mice = 0.01, upper bound mice = 1.5).

903 **7.4.3 Computational modeling**

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

Following Glaze et al.⁵¹, we applied Bayes rule to compute the posterior evidence for the two alternative choices (i.e., the log posterior ratio L) from the sensory evidence available at time-point t (i.e., the log likelihood ratio LLR) with the prior probability ψ , **weighted by the respective precision terms ω_{LLR} and ω_ψ :**

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

In the trial-wise design studied here, a transition between the two states of the environment (i.e., the sources generating the noisy observations available to the participant) can occur at any time. Despite the random nature of the psychophysical paradigms studied here^{20,21}, humans and mice showed significant biases toward preceding choices (Figure 2A and 3A). We thus assumed that the prior probability of the two possible outcomes depends on the posterior choice probability at the preceding trial and the hazard rate H assumed by the participant. Following Glaze et al.⁵¹, the prior ψ is thus computed as follows:

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

In this model, humans, mice and simulated agents make perceptual choices based on noisy observations u . These are computed by applying a sensitivity parameter α to the content of external sensory information s . For humans, we defined the input s by the two alternative states of the environment (stimulus A: $s = 0$; stimulus B: $s = 1$), which generated the observations u through a sigmoid function that applied a sensitivity parameter α :

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

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

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

926 As in humans, we derived the input u by applying a sigmoid function with a sensitivity
 927 parameter α to input s :

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

928 For humans, mice and in simulations, the log likelihood ratio LLR was computed from u as
 929 follows:

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

930 To allow for long-range autocorrelation in stimulus- and history-congruence (Figure 2B and
 931 3B), our modeling approach differed from Glaze et al.⁵¹ in that it allowed for systematic
 932 fluctuation in the impact of sensory information (i.e., LLR) and the prior probability of
 933 choices ψ on the posterior probability L . This was achieved by multiplying the log likelihood
 934 ratio and the log prior ratio with coherent anti-phase fluctuations according to $\omega_{LLR} =$
 935 $a_{LLR} * \sin(f * t + phase) + 1$ and $\omega_\psi = a_\psi * \sin(f * t + phase + \pi) + 1$.

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

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

940 This allowed us to infer the free parameters H (lower bound = 0, upper bound = 1; human

posterior = $0.45 \pm 4.8 \times 10^{-5}$; mouse posterior = $0.46 \pm 2.97 \times 10^{-4}$), α (lower bound = 0, upper bound = 5; human posterior = $0.5 \pm 1.12 \times 10^{-4}$; mouse posterior = $1.06 \pm 2.88 \times 10^{-3}$), a_ψ (lower bound = 0, upper bound = 10; human posterior = $1.44 \pm 5.27 \times 10^{-4}$; mouse posterior = $1.71 \pm 7.15 \times 10^{-3}$), amp_{LLR} (lower bound = 0, upper bound = 10; human posterior = $0.5 \pm 2.02 \times 10^{-4}$; mouse posterior = $0.39 \pm 1.08 \times 10^{-3}$), frequency f (lower bound = 1/40, upper bound = 1/5; human posterior = $0.11 \pm 1.68 \times 10^{-5}$; mouse posterior = $0.11 \pm 1.63 \times 10^{-4}$), p (lower bound = 0, upper bound = 2π ; human posterior = $2.72 \pm 4.41 \times 10^{-4}$; mouse posterior = $2.83 \pm 3.95 \times 10^{-3}$) and inverse decision temperature ζ (lower bound = 1, upper bound = 10; human posterior = $4.63 \pm 1.95 \times 10^{-4}$; mouse posterior = $4.82 \pm 3.03 \times 10^{-3}$) using maximum likelihood estimation with the Broyden–Fletcher–Goldfarb–Shanno algorithm as implemented in the R-function *optimx*⁸⁰ (see **Supplemental Table T2 for a description of our model parameters**).

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

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

- The full *bimodal inference model* (M1; Figure 1F) incorporates the influence of sensory information according to the parameter α (likelihood); the integration of evidence across trials according to the parameter H (prior); anti-phase oscillations in between likelihood and prior precision according to ω_{LLR} and ω_ψ with parameters a_{LLR} (amplitude likelihood fluctuation), a_ψ (amplitude prior fluctuation), f (frequency) and p (phase).
- The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the in-

fluence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior); oscillations in likelihood precision according to ω_{LLR} with parameters a_{LLR} (amplitude likelihood fluctuation), f (frequency) and p (phase).

- The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior); oscillations in the prior precision according to ω_ψ with parameters a_ψ (amplitude prior fluctuation), f (frequency) and p (phase). Please note that all models M1-3 lead to shifts in the relative precision of likelihood and prior.
- The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior), There are no additional oscillations. Model M4 thus corresponds to the model proposed by Glaze et al. and captures normative evidence accumulation in unpredictable environments using a Bayesian update scheme⁵¹. The comparison against M4 tests the null hypothesis that fluctuations in mode emerge from a normative Bayesian model without the ad-hoc addition of oscillations as in models M1-3.
- The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood). The model lacks integration of evidence across trials (flat prior) and oscillations. The comparison against M5 tests the null hypothesis that observers do not use prior information derived from serial dependency in perception.

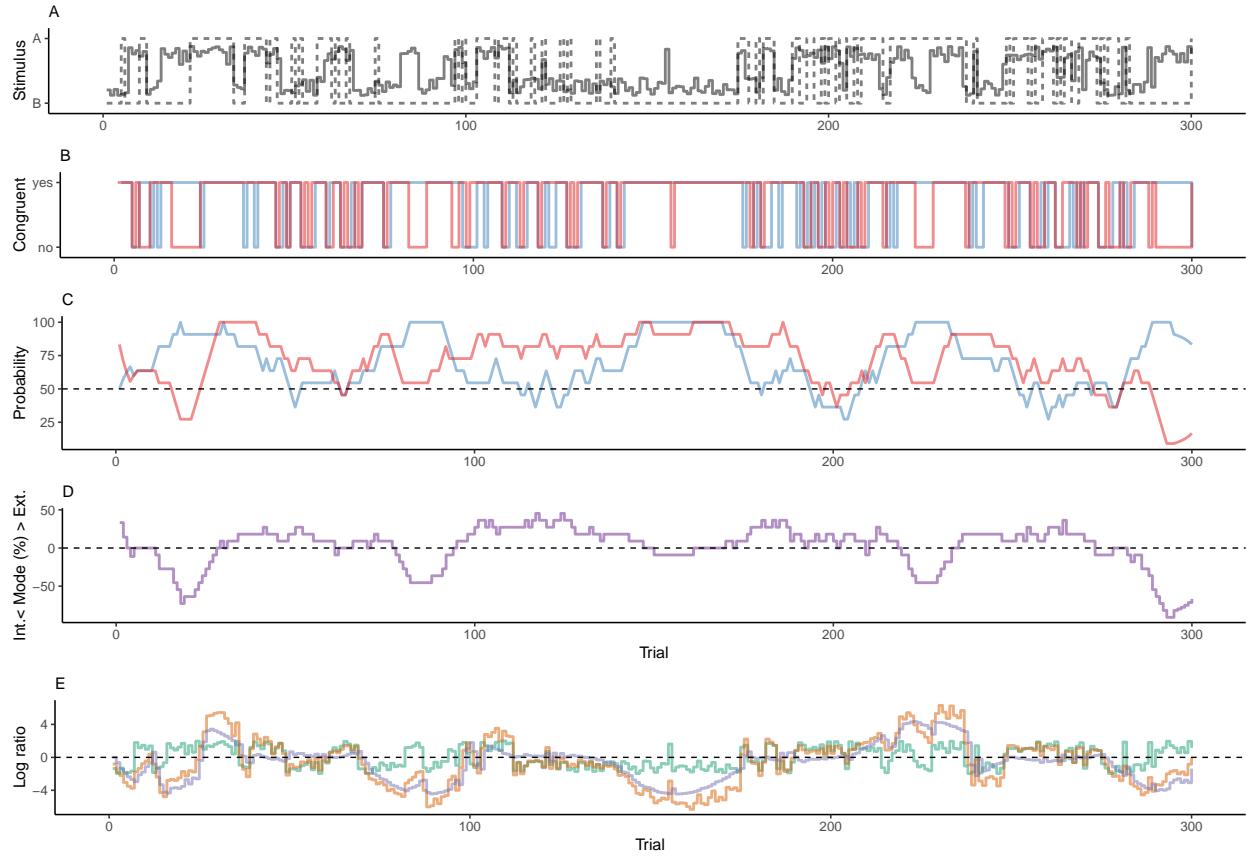
Prediction of within-training and out-of-training variables. To validate our

model, we correlated individual posterior parameter estimates with the respective conventional variables. As a sanity check, we tested (i), whether the estimated hazard rate H correlated negatively with the frequency of history-congruent choices and, (ii), whether the estimated sensitivity to sensory information α correlated positively with the frequency of stimulus-congruent choices. In addition, we tested whether the posterior decision certainty (i.e.. the absolute of the log posterior ratio) correlated negatively with RTs and positively with confidence. This allowed us to assess whether our model could explain aspects of the data it was not fitted to (i.e., RTs and confidence).

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

1018 **8 Figures**

1019 **8.1 Figure 1**



1020 **Figure 1. Concept.**

1021 A. In binary perceptual decision-making, a participant is presented with stimuli from two

1022 categories (A vs. B; dotted line) and reports consecutive perceptual choices via button presses

1023 (solid line). All panels below refer to these simulated example data.

1024

1025 B. When the response matches the external stimulus information (i.e., overlap between

1026 dotted and solid line in panel A), perceptual choices are *stimulus-congruent* (red line). When

1027 the response matches the response at the preceding trial, perceptual choices are *history-*

1028 *congruent* (blue line).

1029 C. The dynamic probabilities of stimulus- and history-congruence (i.e., computed in sliding

1030 windows of ± 5 trials) fluctuate over time.

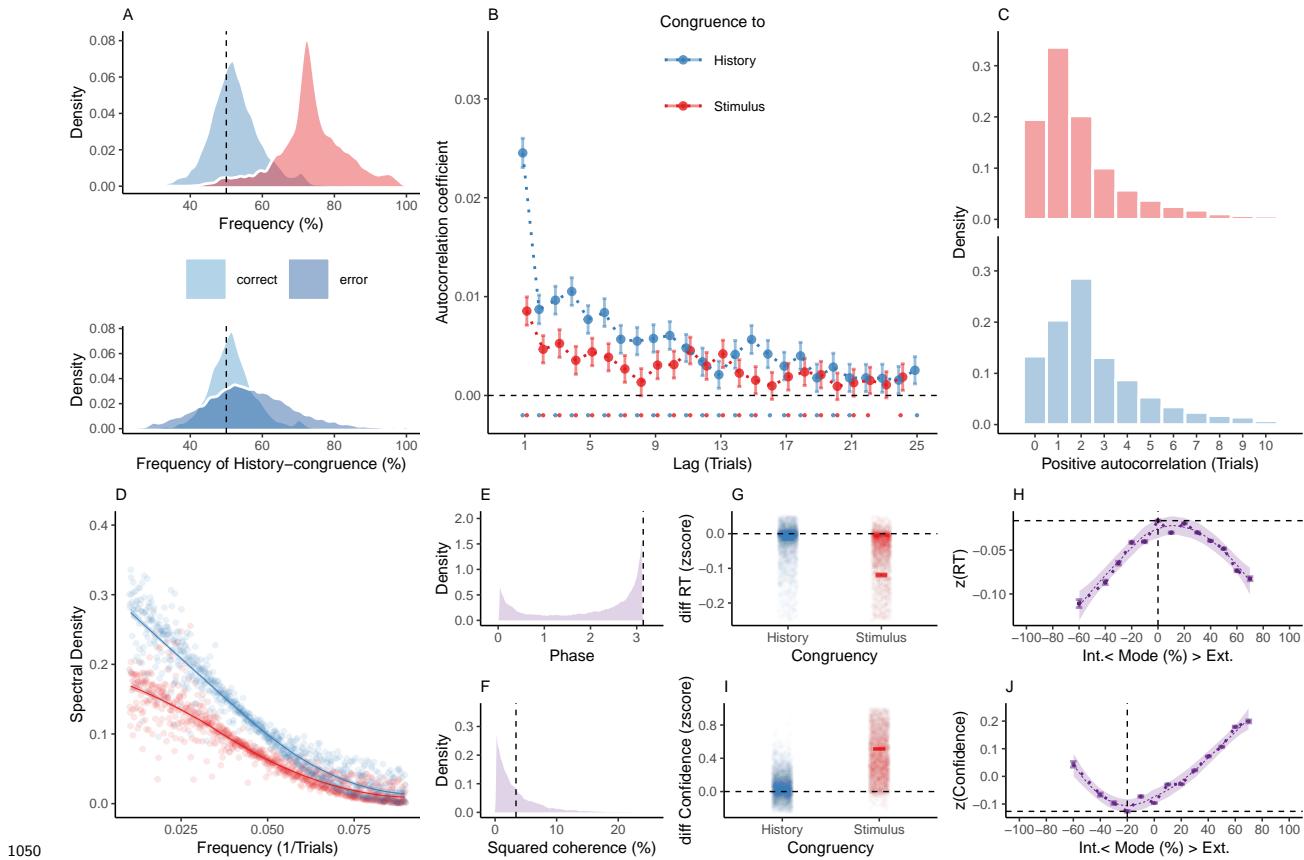
1031 D. The *mode* of perceptual processing is derived by computing the difference between the
1032 dynamic probabilities of stimulus- and history-congruence. Values above 0% indicate a
1033 bias toward external information, whereas values below 0% indicate a bias toward internal
1034 information.

1035 E. In computational modeling, internal mode is caused by an enhanced impact of perceptual
1036 history. This causes the posterior (black line) to be close to the prior (blue line). Conversely,
1037 during external mode, the posterior is close to the sensory information (log likelihood ratio,
1038 red line).

1039 F. The bimodal inference model (M1) explains fluctuations between externally-
1040 and externally-biased modes (left panel) by two interacting factors: a normative
1041 accumulation of evidence according to parameters H (middle panel), and anti-
1042 phase oscillations in the precision terms ω_{LLR} and ω_ψ (right panel).

1043 G. The control models M2-M5 were constructed by successively removing the
1044 anti-phase oscillations and the integration of information from the bimodal in-
1045 ference model. Please note that the normative-evidence-accumulation-model
1046 (M4) corresponds to the model proposed by Glaze et al.⁵¹. In the no-evidence-
1047 accumulation model (M5), perceptual decisions depend only on likelihood infor-
1048 mation (flat priors).

1049 **8.2 Figure 2**



1050 **Figure 2. Internal and external modes in human perceptual decision-making.**

1051 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.

1052 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 $p < 0.05$). Across trials, the autocorrelation coefficients were best fit by an exponential function (adjusted R^2 for stimulus-congruence: 0.53; history-congruence: 0.72) as compared to a linear function (adjusted R^2 for stimulus-congruence: 0.53; history-congruence: 0.51), decaying at a rate of $\gamma = -1.92 \times 10^{-3} \pm 4.5 \times 10^{-4}$

₁₀₆₃ $(T(6.88 \times 10^4) = -4.27, p = 1.98 \times 10^{-5})$ for stimulus-congruence and at a rate of $\gamma =$
₁₀₆₄ $-6.11 \times 10^{-3} \pm 5.69 \times 10^{-4}$ ($T(6.75 \times 10^4) = -10.74, p = 7.18 \times 10^{-27}$) for history-congruence.

₁₀₆₅ C. Here, we depict the number of consecutive trials at which autocorrelation coefficients
₁₀₆₆ exceeded the respective autocorrelation of randomly permuted data within individual partic-
₁₀₆₇ ipants. For stimulus-congruence (upper panel), the lag of positive autocorrelation amounted
₁₀₆₈ to $3.24 \pm 2.39 \times 10^{-3}$ on average, showing a peak at trial $t+1$ after the index trial. For
₁₀₆₉ history-congruence (lower panel), the lag of positive autocorrelation amounted to $4.87 \pm$
₁₀₇₀ 3.36×10^{-3} on average, peaking at trial $t+2$ after the index trial.

₁₀₇₁ D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ± 5
₁₀₇₂ trials) fluctuated as a **scale-invariant process with a 1/f power law**, i.e., at power
₁₀₇₃ densities that were inversely proportional to the frequency.

₁₀₇₄ E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
₁₀₇₅ peaked at half a cycle (π denoted by dotted line).

₁₀₇₆ F. The average squared coherence between fluctuations in stimulus- and history-congruence
₁₀₇₇ (black dotted line) amounted to $6.49 \pm 2.07 \times 10^{-3}\%$

₁₀₇₈ G. We observed faster RTs for both stimulus-congruence (as opposed to stimulus-
₁₀₇₉ incongruence, $\beta = -0.14 \pm 1.6 \times 10^{-3}$, $T(1.99 \times 10^6) = -85.84, p = 0$) and history-
₁₀₈₀ congruence ($\beta = -9.56 \times 10^{-3} \pm 1.37 \times 10^{-3}$, $T(1.98 \times 10^6) = -6.97, p = 3.15 \times 10^{-12}$).

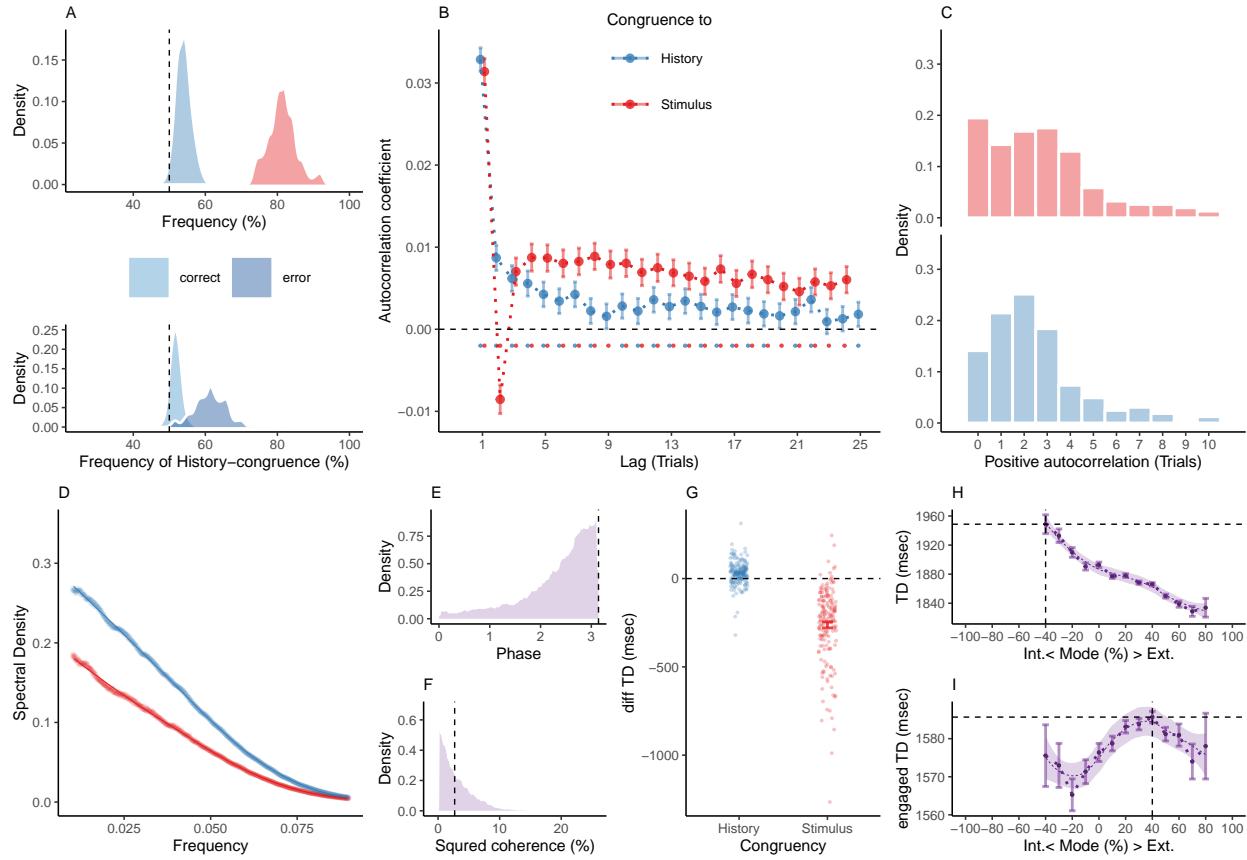
₁₀₈₁ H. The mode of perceptual processing (i.e., the difference between the smoothed probability
₁₀₈₂ of stimulus- vs. history-congruence) showed a quadratic relationship to RTs, with faster
₁₀₈₃ RTs for stronger biases toward both external sensory information and internal predictions
₁₀₈₄ provided by perceptual history ($\beta_2 = -19.86 \pm 0.52$, $T(1.98 \times 10^6) = -38.43, p = 5 \times 10^{-323}$).
₁₀₈₅ The horizontal and vertical dotted lines indicate maximum RT and the associated mode,
₁₀₈₆ respectively.

₁₀₈₇ I. Confidence was enhanced for both stimulus-congruence (as opposed to stimulus-

1088 incongruence, $\beta = 0.48 \pm 1.38 \times 10^{-3}$, $T(2.06 \times 10^6) = 351.54$, $p = 0$) and history-congruence
 1089 ($\beta = 0.04 \pm 1.18 \times 10^{-3}$, $T(2.06 \times 10^6) = 36.85$, $p = 3.25 \times 10^{-297}$).

1090 J. In analogy to RTs, we found a quadratic relationship between the mode of perceptual pro-
 1091 cessing and confidence, which increased when both externally- and internally-biased modes
 1092 grew stronger ($\beta_2 = 39.3 \pm 0.94$, $T(2.06 \times 10^6) = 41.95$, $p = 0$). The horizontal and vertical
 1093 dotted lines indicate minimum confidence and the associated mode, respectively.

1094 8.3 Figure 3



1096 **Figure 3. Internal and external modes in mouse perceptual decision-making.**

1097 A. In mice, $81.37\% \pm 0.3\%$ of trials were stimulus-congruent (in red) and $54.03\% \pm 0.17\%$ of
 1098 trials were history-congruent (in blue; upper panel). History-congruent perceptual choices
 1099 were not a consequence of the experimental design, but a source of error, as they were more
 1100 frequent on stimulus-incongruent trials (lower panel).

1101 B. Relative to randomly permuted data, we found highly significant autocorrelations of
1102 stimulus-congruence and history-congruence (dots indicate intercepts $\neq 0$ in trial-wise lin-
1103 ear mixed effects modeling at $p < 0.05$). Please note that the negative autocorrelation of
1104 stimulus-congruence at trial 2 was a consequence of the experimental design (Supplemental
1105 Figure 2D-F). As in humans, autocorrelation coefficients were best fit by an exponential
1106 function (adjusted R^2 for stimulus-congruence: 0.44; history-congruence: 0.52) as compared
1107 to a linear function (adjusted R^2 for stimulus-congruence: 3.16×10^{-3} ; history-congruence:
1108 0.26), decaying at a rate of $\gamma = -6.2 \times 10^{-4} \pm 5.93 \times 10^{-4}$ ($T(3.55 \times 10^4) = -1.05$, $p =$
1109 0.3) for stimulus-congruence and at a rate of $\gamma = -6.7 \times 10^{-3} \pm 5.94 \times 10^{-4}$ ($T(3.69 \times 10^4)$
1110 $= -11.27$, $p = 2.07 \times 10^{-29}$) for history-congruence.

1111 C. For stimulus-congruence (upper panel), the lag of positive autocorrelation was longer
1112 in comparison to humans (4.59 ± 0.06 on average). For history-congruence (lower panel),
1113 the lag of positive autocorrelation was slightly shorter relative to humans (2.58 ± 0.01 on
1114 average, peaking at trial t+2 after the index trial).

1115 D. In mice, the dynamic probabilities of stimulus- and history-congruence (sliding windows
1116 of ± 5 trials) fluctuated as **a scale-invariant process with a 1/f power law**.

1117 E. The distribution of phase shift between fluctuations in stimulus- and history-congruence
1118 peaked at half a cycle (π denoted by dotted line).

1119 F. The average squared coherence between fluctuations in stimulus- and history-congruence
1120 (black dotted line) amounted to $3.45 \pm 0.01\%$.

1121 G. We observed shorter trial durations (TDs) for stimulus-congruence (as opposed to
1122 stimulus-incongruence, $\beta = -1.12 \pm 8.53 \times 10^{-3}$, $T(1.34 \times 10^6) = -131.78$, $p = 0$), but
1123 longer TDs for history-congruence ($\beta = 0.06 \pm 6.76 \times 10^{-3}$, $T(1.34 \times 10^6) = 8.52$, $p =$
1124 1.58×10^{-17}).

1125 H. TDs decreased monotonically for stronger biases toward external mode ($\beta_1 = -4.16 \times 10^4$
1126 $\pm 1.29 \times 10^3$, $T(1.35 \times 10^6) = -32.31$, $p = 6.03 \times 10^{-229}$). The horizontal and vertical dotted

₁₁₂₇ lines indicate maximum TD and the associated mode, respectively.

₁₁₂₈ I. For TDs that differed from the median TD by no more than $1.5 \times$ MAD (median absolute

₁₁₂₉ distance⁴⁹), mice exhibited a quadratic component in the relationship between the mode of

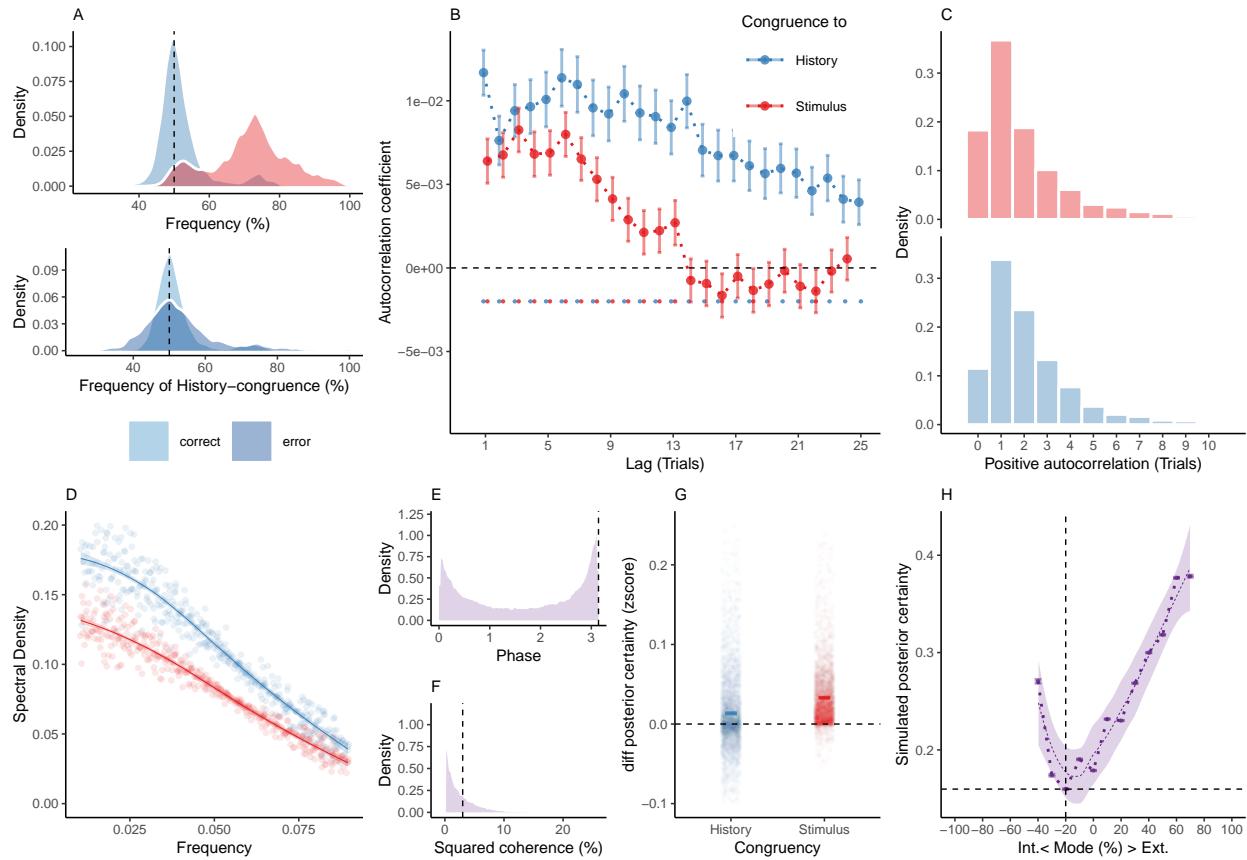
₁₁₃₀ sensory processing and TDs ($\beta_2 = -1.97 \times 10^3 \pm 843.74$, $T(1.19 \times 10^6) = -2.34$, $p = 0.02$).

₁₁₃₁ This explorative post-hoc analysis focuses on trials at which mice engage more swiftly with

₁₁₃₂ the experimental task. The horizontal and vertical dotted lines indicate maximum TD and

₁₁₃₃ the associated mode, respectively.

1134 **8.4 Figure 4**



1135 **Figure 4. Internal and external modes in simulated perceptual decision-making.**

1136 A. Simulated perceptual choices were stimulus-congruent in $71.36\% \pm 0.17\%$ (in red) and
 1137 history-congruent in $51.99\% \pm 0.11\%$ of trials (in blue; $T(4.32 \times 10^3) = 17.42$, $p = 9.89 \times$
 1138 10^{-66} ; upper panel). Due to the competition between stimulus- and history-congruence,
 1139 history-congruent perceptual choices were more frequent when perception was stimulus-
 1140 incongruent (i.e., on *error* trials; $T(4.32 \times 10^3) = 11.19$, $p = 1.17 \times 10^{-28}$; lower panel)
 1141 and thus impaired performance in the randomized psychophysical design simulated here.
 1142

1143 B. At the simulated group level, we found significant autocorrelations in both stimulus-
 1144 congruence (13 consecutive trials) and history-congruence (30 consecutive trials).

1145 C. On the level of individual simulated participants, autocorrelation coefficients exceeded the
 1146 autocorrelation coefficients of randomly permuted data within a lag of $2.46 \pm 1.17 \times 10^{-3}$

₁₁₄₇ trials for stimulus-congruence and $4.24 \pm 1.85 \times 10^{-3}$ trials for history-congruence.

₁₁₄₈ D. The smoothed probabilities of stimulus- and history-congruence (sliding windows of ± 5
₁₁₄₉ trials) fluctuated as a **scale-invariant process with a $1/f$ power law**, i.e., at power den-
₁₁₅₀ sities that were inversely proportional to the frequency (power $\sim 1/f^\beta$; stimulus-congruence:
₁₁₅₁ $\beta = -0.81 \pm 1.18 \times 10^{-3}$, $T(1.92 \times 10^5) = -687.58$, $p = 0$; history-congruence: $\beta = -0.83$
₁₁₅₂ $\pm 1.27 \times 10^{-3}$, $T(1.92 \times 10^5) = -652.11$, $p = 0$).

₁₁₅₃ E. The distribution of phase shift between fluctuations in simulated stimulus- and history-
₁₁₅₄ congruence peaked at half a cycle (π denoted by dotted line). The dynamic probabilities of
₁₁₅₅ simulated stimulus- and history-congruence were therefore were strongly anti-correlated (β
₁₁₅₆ $= -0.03 \pm 8.22 \times 10^{-4}$, $T(2.12 \times 10^6) = -40.52$, $p = 0$).

₁₁₅₇ F. The average squared coherence between fluctuations in simulated stimulus- and history-
₁₁₅₈ congruence (black dotted line) amounted to $6.49 \pm 2.07 \times 10^{-3}\%$.

₁₁₅₉ G. Simulated confidence was enhanced for stimulus-congruence ($\beta = 0.03 \pm 1.71 \times 10^{-4}$,
₁₁₆₀ $T(2.03 \times 10^6) = 178.39$, $p = 0$) and history-congruence ($\beta = 0.01 \pm 1.5 \times 10^{-4}$, $T(2.03 \times 10^6)$
₁₁₆₁ $= 74.18$, $p = 0$).

₁₁₆₂ H. In analogy to humans, the simulated data showed a quadratic relationship between the
₁₁₆₃ mode of perceptual processing and posterior certainty, which increased for stronger external
₁₁₆₄ and internal biases ($\beta_2 = 31.03 \pm 0.15$, $T(2.04 \times 10^6) = 205.95$, $p = 0$). The horizontal
₁₁₆₅ and vertical dotted lines indicate minimum posterior certainty and the associated mode,
₁₁₆₆ respectively.

₁₁₆₇ **9 Supplemental Items**

₁₁₆₈ **9.1 Internal mode processing is driven by choice history as op-**
₁₁₆₉ **posed to stimulus history**

₁₁₇₀ The main manuscript reports the effects of perceptual history, which we defined
₁₁₇₁ as the impact of the choice at the preceding trial on the choice at the current trial
₁₁₇₂ (henceforth *choice history*). *Stimulus history*, which is defined as the impact
₁₁₇₃ of the stimulus presented at the preceding trial on the choice at the present
₁₁₇₄ trial, represents an alternative approach to this. Here, we compare the effects
₁₁₇₅ of choice history to the effects of stimulus history.

₁₁₇₆ We observed a significant bias toward stimulus history (humans: $49.76\% \pm 0.1\%$
₁₁₇₇ of trials, $\beta = 1.26 \pm 0.94$, $T(373.62) = 1.34$, $p = 0.18$; mice: $51.11\% \pm 0.08\%$ of
₁₁₇₈ trials, $T(164) = 13.4$, $p = 3.86 \times 10^{-28}$). The bias toward stimulus history was
₁₁₇₉ smaller than the bias toward choice history (humans: $\beta = -3.53 \pm 0.5$, $T(66.53)$
₁₁₈₀ $= -7.01$, $p = 1.48 \times 10^{-9}$; mice: $T(164) = -17.21$, $p = 1.43 \times 10^{-38}$).

₁₁₈₁ The attraction of choices toward both preceding choices and stimuli is expected,
₁₁₈₂ as perception was *stimulus-congruent* on approximately 75% of trials, causing
₁₁₈₃ choices and stimuli to be highly correlated. We therefore compared the effects
₁₁₈₄ of choice history and stimulus history after *stimulus-incongruent* (i.e., *error*)
₁₁₈₅ trials, since those trials lead to opposite predictions regarding the perceptual
₁₁₈₆ choice at the subsequent trial.

₁₁₈₇ As expected from the findings presented in the main manuscript, perceptual
₁₁₈₈ choices were attracted toward perceptual choices when the inducing trial was
₁₁₈₉ stimulus-incongruent (i.e., a positive effect of choice history; humans: $\beta = 0.19$
₁₁₉₀ $\pm 1.4 \times 10^{-4}$, $z = 1.36 \times 10^3$, $p = 0$; mice: $\beta = 0.92 \pm 0.01$, $z = 88.82$, $p = 0$). By
₁₁₉₁ contrast, perceptual choices tended to be repelled away from the stimulus pre-

1192 sented at preceding stimulus-incongruent trial (i.e., a negative effect of stimulus
1193 history; humans: $\beta = -0.19 \pm 0.01$, $z = -16.47$, $p = 5.99 \times 10^{-61}$; mice: $\beta = -0.92$
1194 ± 0.01 , $z = -88.76$, $p = 0$). This repulsion of choices away from stimuli presented
1195 at stimulus-incongruent trials confirmed that choices (which are anti-correlated
1196 to stimuli at stimulus-incongruent trials) were the primary driver of attracting
1197 serial effects in perception.

1198 In sum, the above results suggest that, in both humans and mice, serial depen-
1199 dencies were better explained by the effects of choice history as opposed to the
1200 effects of stimulus history. This aligns with a result recently published for the
1201 IBL database, where mice were shown to follow an *action-kernel* as opposed to
1202 a *stimulus-kernel* model when integrating information across trials⁸¹.

1203 **9.2 Fluctuations between internal and external mode modulate
1204 perceptual performance beyond the effect of general response
1205 biases**

1206 The hypothesis that perception cycles through opposing internally- and externally-biased
1207 modes is motivated by the assumption that recurring intervals of stronger perceptual history
1208 temporally reduce the participants' sensitivity to external information. Importantly, the
1209 history-dependent biases that characterize internal mode processing must be differentiated
1210 from general response biases. In binary perceptual decision-making, general response biases
1211 are defined by a propensity to choose one of the two outcomes more often than the alternative.
1212 Indeed, human participants selected the more frequent of the two possible outcomes in 58.71%
1213 $\pm 0.22\%$ of trials, and mice selected the more frequent of the two possible outcomes in 54.6%
1214 $\pm 0.3\%$ of trials.

1215 Two caveats have to be considered to make sure that the effect of history-congruence is
1216 distinct from the effect of general response biases. First, history-congruent states become

more likely for larger response biases that cause an increasing imbalance in the likelihood of the two outcomes (humans: $\beta = 0.24 \pm 6.93 \times 10^{-4}$, $T(2.09 \times 10^6) = 342.43$, $p = 0$; mice: $\beta = 0.15 \pm 8.25 \times 10^{-4}$, $T(1.32 \times 10^6) = 181.93$, $p = 0$). 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 ± 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: $\beta_1 = -0.05 \pm 5.63 \times 10^{-4}$, $T(2.1 \times 10^6) = -84.21$, $p = 0$; mice: $\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$, $p = 0$) beyond the effect of ongoing changes in general response biases (humans: $\beta_2 = -0.06 \pm 5.82 \times 10^{-4}$, $T(2.1 \times 10^6) = -103.51$, $p = 0$; mice: $\beta_2 = -0.03 \pm 6.94 \times 10^{-4}$, $T(1.34 \times 10^6) = -48.14$, $p = 0$). 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

₁₂₄₃ biases.

₁₂₄₄ 9.3 Internal mode is characterized by lower thresholds as well as ₁₂₄₅ by history-dependent changes in biases and lapses

₁₂₄₆ Random or stereotypical responses may provide an alternative explanation for the reduced
₁₂₄₇ sensitivity to external sensory information that we attribute to internal mode processing. To
₁₂₄₈ test this hypothesis, we asked whether history-independent changes in biases and lapses may
₁₂₄₉ provide an alternative explanation of the reduced sensitivity during internal mode.

₁₂₅₀ To this end, we estimated full and history-conditioned psychometric curves to investigate
₁₂₅₁ how internal and external mode relate to biases (i.e., the horizontal position of the psycho-
₁₂₅₂ metric curve), lapses (i.e., the asymptotes of the psychometric curve) and thresholds (i.e.,
₁₂₅₃ 1/sensitivity, estimated from the slope of the psychometric curve). We used a maximum
₁₂₅₄ likelihood procedure to predict trial-wise choices y ($y = 0$ and $y = 1$ for outcomes A and B
₁₂₅₅ respectively) from the choice probabilities y_p . y_p was computed from the difficulty-weighted
₁₂₅₆ inputs s_w via a parametric error function defined by the parameters γ (lower lapse), δ (upper
₁₂₅₇ lapse), μ (bias) and t (threshold; see Methods for details):

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

₁₂₅₈ Under our main hypothesis that periodic reductions in sensitivity to external information
₁₂₅₉ are driven by increases in the impact of perceptual history, one would expect (i) a history-
₁₂₆₀ dependent increase in biases and lapses (effects of perceptual history), and (ii), a history-
₁₂₆₁ independent increase in threshold (reduced sensitivity to external information). Conversely,
₁₂₆₂ if what we identified as internal mode processing was in fact driven by random choices, one
₁₂₆₃ would expect (i), a history-independent increase in lapse (choice randomness), (ii), no change
₁₂₆₄ in bias (no effect of perceptual history), and (iii), reduced thresholds (reduced sensitivity to

₁₂₆₅ external information).

₁₂₆₆ 9.3.1 Humans

₁₂₆₇ Across all data provided by the Confidence database²⁰ (i.e., irrespective of the preceding
₁₂₆₈ perceptual choice y_{t-1}), biases μ were distributed around zero (-0.05 ± 0.03 ; $\beta_0 = 7.37 \times$
₁₂₆₉ $10^{-3} \pm 0.09$, $T(36.8) = 0.08$, $p = 0.94$; Supplemental Figure 6A-B, upper panel). When
₁₂₇₀ conditioned on perceptual history, biases μ varied according to the preceding perceptual
₁₂₇₁ choice, with negative biases for $y_{t-1} = 0$ (-0.22 ± 0.04 ; $\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$,
₁₂₇₂ $p = 3.64 \times 10^{-5}$; Supplemental Figure 6A-B, upper panel) and positive biases for $y_{t-1} = 1$
₁₂₇₃ (0.29 ± 0.03 ; $\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$; Supplemental Figure 6A-B,
₁₂₇₄ lower panel). Absolute biases $|\mu|$ were larger in internal mode (1.84 ± 0.03) as compared
₁₂₇₅ to external mode (0.86 ± 0.02 ; $\beta_0 = -0.62 \pm 0.07$, $T(45.62) = -8.38$, $p = 8.59 \times 10^{-11}$;
₁₂₇₆ controlling for differences in lapses and thresholds).

₁₂₇₇ Lower and upper lapses amounted to $\gamma = 0.13 \pm 2.83 \times 10^{-3}$ and $\delta = 0.1 \pm 2.45 \times 10^{-3}$
₁₂₇₈ (Supplemental Figure 6A, C and D). Lapses were larger in internal mode ($\gamma = 0.17 \pm 3.52 \times$
₁₂₇₉ 10^{-3} , $\delta = 0.14 \pm 3.18 \times 10^{-3}$) as compared to external mode ($\gamma = 0.1 \pm 2.2 \times 10^{-3}$, $\delta =$
₁₂₈₀ $0.08 \pm 2 \times 10^{-3}$; $\beta_0 = -0.05 \pm 5.73 \times 10^{-3}$, $T(47.03) = -9.11$, $p = 5.94 \times 10^{-12}$; controlling
₁₂₈₁ for differences in biases and thresholds).

₁₂₈₂ Conditioning on the previous perceptual choice revealed that the between-mode difference
₁₂₈₃ in lapse was not general, but depended on perceptual history: For $y_{t-1} = 0$, only higher
₁₂₈₄ lapses δ differed between internal and external mode ($\beta_0 = -0.1 \pm 9.58 \times 10^{-3}$, $T(36.87) =$
₁₂₈₅ -10.16 , $p = 3.06 \times 10^{-12}$), whereas lower lapses γ did not ($\beta_0 = 0.01 \pm 7.77 \times 10^{-3}$, $T(33.1)$
₁₂₈₆ $= 1.61$, $p = 0.12$). Vice versa, for $y_{t-1} = 1$, lower lapses γ differed between internal and
₁₂₈₇ external mode ($\beta_0 = -0.11 \pm 0.01$, $T(40.11) = -9.59$, $p = 6.14 \times 10^{-12}$), whereas higher
₁₂₈₈ lapses δ did not ($\beta_0 = 0.01 \pm 7.74 \times 10^{-3}$, $T(33.66) = 1.58$, $p = 0.12$).

₁₂₈₉ Thresholds t were estimated at 3 ± 0.06 (Supplemental Figure 6A and E). Thresholds t were

1290 larger in internal mode (3.66 ± 0.09) as compared to external mode (2.02 ± 0.03 ; $\beta_0 = -1.77$
1291 ± 0.25 , $T(50.45) = -7.14$, $p = 3.48 \times 10^{-9}$; controlling for differences in biases and lapses).
1292 In contrast to the bias μ and the lapse rates γ and δ , thresholds t were not modulated by
1293 perceptual history ($\beta_0 = 0.04 \pm 0.06$, $T(2.97 \times 10^3) = 0.73$, $p = 0.47$).

1294 **9.3.2 Mice**

1295 When estimated based on the full dataset provided in the IBL database²¹ (i.e., irrespective
1296 of the preceding perceptual choice y_{t-1}), biases μ were distributed around zero (3.87×10^{-3}
1297 $\pm 9.81 \times 10^{-3}$; $T(164) = 0.39$, $p = 0.69$; Supplemental Figure 7A-B, upper panel). When
1298 conditioned on the preceding perceptual choice, biases were negative for $y_{t-1} = 0$ (-0.02
1299 $\pm 8.7 \times 10^{-3}$; $T(164) = -1.99$, $p = 0.05$; Supplemental Figure 7A-B, middle panel) and
1300 positive for $y_{t-1} = 1$ ($0.02 \pm 9.63 \times 10^{-3}$; $T(164) = 1.91$, $p = 0.06$; Supplemental Figure
1301 7A-B, lower panel). As in humans, mice showed larger biases during internal mode ($0.14 \pm$
1302 7.96×10^{-3}) as compared to external mode ($0.07 \pm 8.7 \times 10^{-3}$; $\beta_0 = -0.18 \pm 0.03$, $T =$
1303 -6.38 , $p = 1.77 \times 10^{-9}$; controlling for differences in lapses and thresholds).

1304 Lower and upper lapses amounted to $\gamma = 0.1 \pm 4.35 \times 10^{-3}$ and $\delta = 0.11 \pm 4.65 \times 10^{-3}$
1305 (Supplemental Figure 7A, C and D). Lapse rates were higher in internal mode ($\gamma = 0.15 \pm$
1306 5.14×10^{-3} , $\delta = 0.16 \pm 5.79 \times 10^{-3}$) as compared to external mode ($\gamma = 0.06 \pm 3.11 \times 10^{-3}$,
1307 $\delta = 0.07 \pm 3.34 \times 10^{-3}$; $\beta_0 = -0.11 \pm 4.39 \times 10^{-3}$, $T = -24.8$, $p = 4.91 \times 10^{-57}$; controlling
1308 for differences in biases and thresholds).

1309 For $y_{t-1} = 0$, the difference between internal and external mode was more pronounced for
1310 higher lapses δ ($T(164) = 21.44$, $p = 1.93 \times 10^{-49}$). Conversely, for $y_{t-1} = 1$, the difference
1311 between internal and external mode was more pronounced for lower lapses γ ($T(164) =$
1312 -18.24 , $p = 2.68 \times 10^{-41}$). In contrast to the human data, higher lapses δ and lower lapses
1313 γ were significantly elevated during internal mode irrespective of the preceding perceptual
1314 choice (higher lapses δ for $y_{t-1} = 1$: $T(164) = -2.65$, $p = 8.91 \times 10^{-3}$; higher lapses δ for
1315 $y_{t-1} = 0$: $T(164) = -28.29$, $p = 5.62 \times 10^{-65}$; lower lapses γ for $y_{t-1} = 1$: $T(164) = -32.44$,

₁₃₁₆ $p = 2.92 \times 10^{-73}$; lower lapses γ for $y_{t-1} = 0$: $T(164) = -2.5$, $p = 0.01$.

₁₃₁₇ In mice, thresholds t amounted to $0.15 \pm 6.52 \times 10^{-3}$ (Supplemental Figure 7A and E) and
₁₃₁₈ were higher in internal mode (0.27 ± 0.01) as compared to external mode ($0.09 \pm 4.44 \times 10^{-3}$;
₁₃₁₉ $\beta_0 = -0.28 \pm 0.04$, $T = -7.26$, $p = 1.53 \times 10^{-11}$; controlling for differences in biases and
₁₃₂₀ lapses). Thresholds t were not modulated by perceptual history ($T(164) = 0.94$, $p = 0.35$).

₁₃₂₁ In sum, the above analyses showed that, in both humans and mice, internal and external
₁₃₂₂ mode differ with respect to biases, lapses and thresholds. Internally-biased processing was
₁₃₂₃ characterized by higher thresholds, indicating a reduced sensitivity to sensory information,
₁₃₂₄ as well as by larger biases and lapses. Importantly, between-mode differences in biases
₁₃₂₅ and lapses strongly depended on perceptual history. This confirmed that internal mode
₁₃₂₆ processing cannot be explained solely on the ground of a general (i.e., history-independent)
₁₃₂₇ increase in lapses or bias indicative of random or stereotypical responses.

₁₃₂₈ **9.4 Internal mode processing can not be reduced to insufficient 1329 task familiarity**

₁₃₃₀ It may be assumed that participants tend to repeat preceding choices when they are not yet
₁₃₃₁ familiar with the experimental task, leading to history-congruent choices that are caused by
₁₃₃₂ insufficient training. To assess this alternative explanation, we contrasted the correlates of
₁₃₃₃ bimodal inference with training effects in humans and mice.

₁₃₃₄ **9.4.1 Humans**

₁₃₃₅ In the Confidence database²⁰, training effects were visible from RTs that were shortened by
₁₃₃₆ 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
₁₃₃₇ $= 0$). Intriguingly, however, history-congruent choices became more frequent with increased
₁₃₃₈ exposure to the task ($\beta = 3.6 \times 10^{-5} \pm 2.54 \times 10^{-6}$, $z = 14.19$, $p = 10^{-45}$), speaking against
₁₃₃₉ the proposition that insufficient training induces seriality in response behavior.

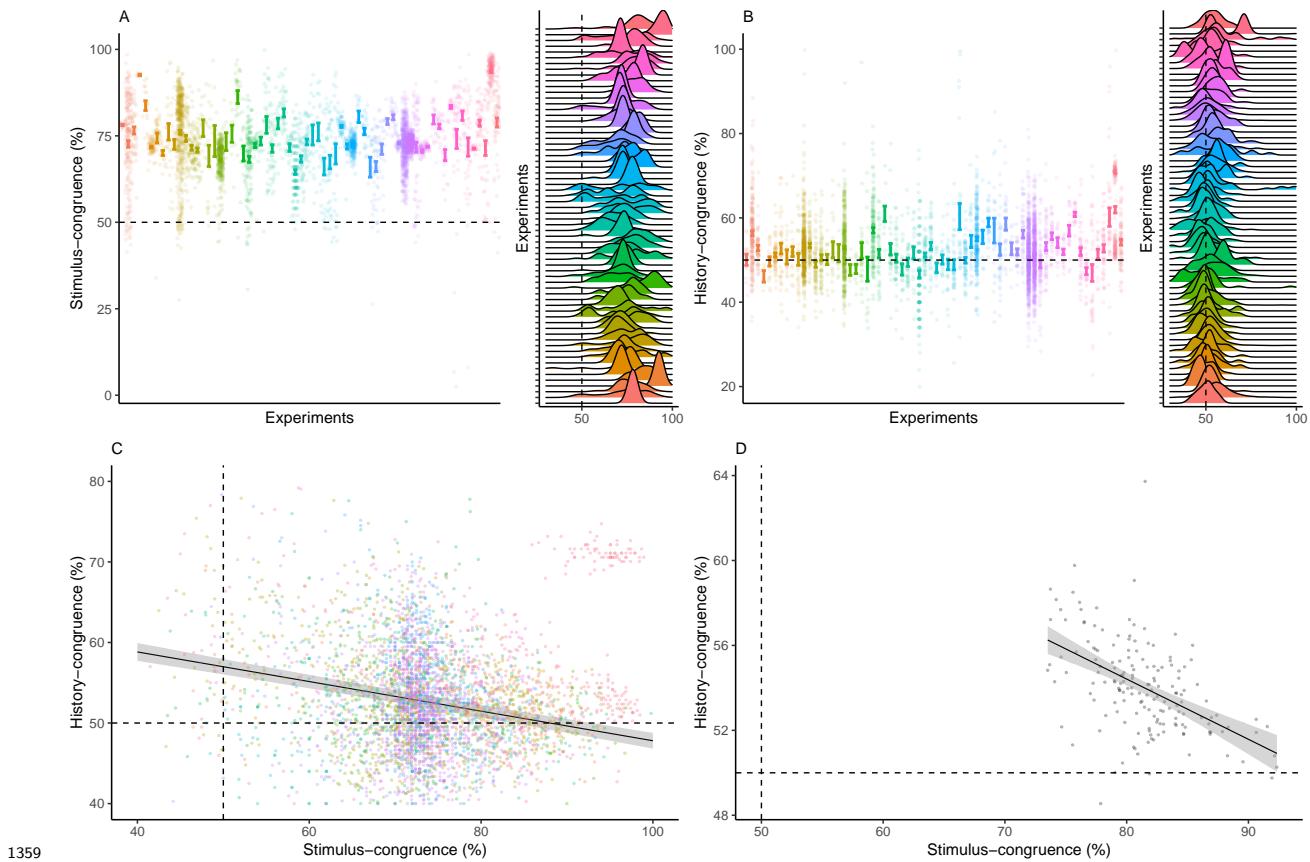
₁₃₄₀ **9.4.2 Mice**

₁₃₄₁ As in humans, it is an important caveat to consider whether the observed serial dependencies
₁₃₄₂ in mice reflect a phenomenon of perceptual inference, or, alternatively, an unspecific strategy
₁₃₄₃ that occurs at the level of reporting behavior. We reasoned that, if mice indeed tended to
₁₃₄₄ repeat previous choices as a general response pattern, history effects should decrease during
₁₃₄₅ training of the perceptual task. We therefore analyzed how stimulus- and history-congruent
₁₃₄₆ perceptual choices evolved across sessions in mice that, by the end of training, achieved
₁₃₄₇ proficiency (i.e., stimulus-congruence $\geq 80\%$) in the *basic* task of the IBL dataset²¹.

₁₃₄₈ Across sessions, we found that stimulus-congruent perceptual choices became more frequent
₁₃₄₉ ($\beta = 0.34 \pm 7.13 \times 10^{-3}$, $T(8.51 \times 10^3) = 47.66$, $p = 0$) and TDs were progressively shortened
₁₃₅₀ ($\beta = -22.14 \pm 17.06$, $T(1.14 \times 10^3) = -1.3$, $p = 0$). Crucially, the frequency of history-
₁₃₅₁ congruent perceptual choices also increased during training ($\beta = 0.13 \pm 4.67 \times 10^{-3}$, $T(8.4 \times$
₁₃₅₂ $10^3) = 27.04$, $p = 1.96 \times 10^{-154}$; Supplemental Figure S8).

₁₃₅₃ Within individual session, longer task exposure was associated with an increase in history-
₁₃₅₄ congruence ($\beta = 3.6 \times 10^{-5} \pm 2.54 \times 10^{-6}$, $z = 14.19$, $p = 10^{-45}$) and a decrease in TDs (β
₁₃₅₅ $= -0.1 \pm 3.96 \times 10^{-3}$, $T(1.34 \times 10^6) = -24.99$, $p = 9.45 \times 10^{-138}$). In sum, these findings
₁₃₅₆ strongly argue against the proposition that mice show biases toward perceptual history due
₁₃₅₇ to an unspecific response strategy.

1358 **9.5 Supplemental Figure S1**



1360 **Supplemental Figure S1. Stimulus- and history-congruence.**

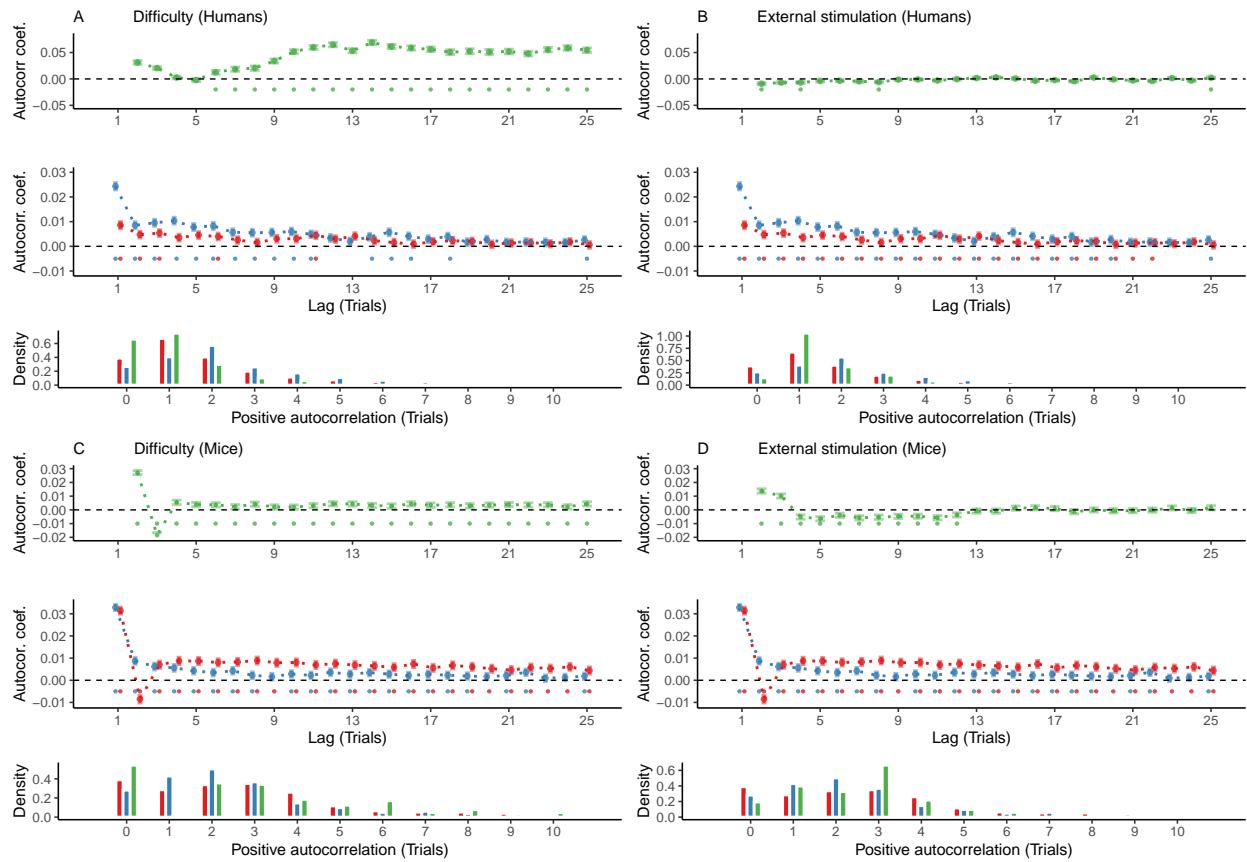
1361 A. Stimulus-congruent choices in humans amounted to $73.46\% \pm 0.15\%$ of trials and were
1362 highly consistent across the experiments selected from the Confidence Database.

1363 B. History-congruent choices in humans amounted to $52.7\% \pm 0.12\%$ of trials. In analogy
1364 to stimulus-congruence, the prevalence of history-congruence was highly consistent across
1365 the experiments selected from the Confidence Database. 48.48% of experiments showed
1366 significant ($p < 0.05$) biases toward preceding choices, whereas 2 of the 66 of the included
1367 experiments showed significant repelling biases.

1368 C. In humans, we found an enhanced impact of perceptual history in participants who were
1369 less sensitive to external sensory information ($T(4.3 \times 10^3) = -14.27$, $p = 3.78 \times 10^{-45}$),
1370 suggesting that perception results from the competition of external with internal information.

₁₃₇₁ D. In analogy to humans, mice that were less sensitive to external sensory information
₁₃₇₂ showed stronger biases toward perceptual history ($T(163) = -7.52$, $p = 3.44 \times 10^{-12}$, Pearson
₁₃₇₃ correlation).

1374 **9.6 Supplemental Figure S2**



1375

1376 **Supplemental Figure S2. Controlling for task difficulty and external stimulation.**

1377 In this study, we found highly significant autocorrelations of stimulus- and history-
 1378 congruence in humans as well as in mice, while controlling for task difficulty and the
 1379 sequence of external stimulation. **Here, we confirm that the autocorrelations of**
 1380 **stimulus- and history-congruence were not a trivial consequence of the exper-**
 1381 **imental design or the addition of task difficulty and external stimulation as**
 1382 **control variables in the computation of group-level autocorrelations.**

1383 A. In humans, task difficulty (in green) showed a significant autocorrelation starting at the
 1384 5th trial (upper panel, dots at the bottom indicate intercepts $\neq 0$ in trial-wise linear mixed
 1385 effects modeling at $p < 0.05$). When controlling for task difficulty only, linear mixed effects
 1386 modeling indicated a significant autocorrelation of stimulus-congruence (in red) for the first
 1387 3 consecutive trials (middle panel). 20% of trials within the displayed time window remained

1388 significantly autocorrelated. The autocorrelation of history-congruence (in blue) remained
1389 significant for the first 11 consecutive trials (64% significantly autocorrelated trials within
1390 the displayed time window). At the level of individual participants, the autocorrelation of
1391 task difficulty exceeded the respective autocorrelation of randomly permuted within a lag of
1392 $21.66 \pm 8.37 \times 10^{-3}$ trials (lower panel).

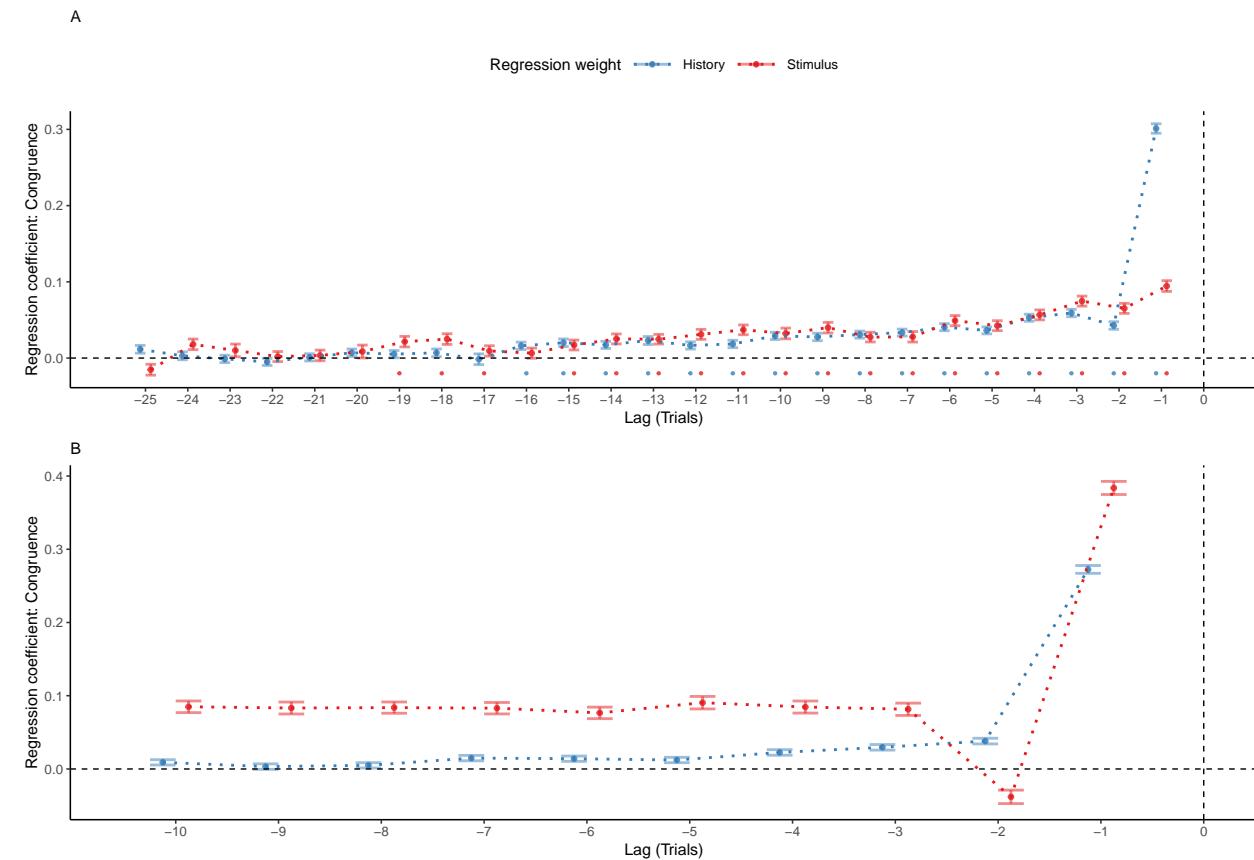
1393 B. In humans, the sequence of external stimulation (i.e., which of the two binary outcomes
1394 was supported by the presented stimuli; depicted in green) was negatively autocorrelated
1395 for 1 trial. When controlling for the autocorrelation of external stimulation only, stimulus-
1396 congruence remained significantly autocorrelated for 22 consecutive trials (88% of trials
1397 within the displayed time window; lower panel) and history-congruence remained significantly
1398 autocorrelated for 20 consecutive trials (84% of trials within the displayed time window). At
1399 the level of individual participants, the autocorrelation of external stimulation exceeded the
1400 respective autocorrelation of randomly permuted within a lag of $2.94 \pm 4.4 \times 10^{-3}$ consecutive
1401 trials (lower panel).

1402 C. In mice, task difficulty showed a significant autocorrelation for the first 25 consecutive trials
1403 (upper panel). When controlling only for task difficulty only, linear mixed effects modeling
1404 indicated a significant autocorrelation of stimulus-congruence for the first 36 consecutive
1405 trials (middle panel). In total, 100% of trials within the displayed time window remained
1406 significantly autocorrelated. The autocorrelation of history-congruence remained significant
1407 for the first 8 consecutive trials, with 84% significantly autocorrelated trials within the dis-
1408 played time window. At the level of individual mice, autocorrelation coefficients for difficulty
1409 were elevated above randomly permuted data within a lag of 15.13 ± 0.19 consecutive trials
1410 (lower panel).

1411 D. In mice, the sequence of external stimulation (i.e., which of the two binary outcomes
1412 was supported by the presented stimuli) was negatively autocorrelated for 11 consecutive
1413 trials (upper panel). When controlling only for the autocorrelation of external stimulation,

₁₄₁₄ stimulus-congruence remained significantly autocorrelated for 86 consecutive trials (100% of
₁₄₁₅ trials within the displayed time window; middle) and history-congruence remained signifi-
₁₄₁₆ cantly autocorrelated for 8 consecutive trials (84% of trials within the displayed time window).
₁₄₁₇ At the level of individual mice, autocorrelation coefficients for external stimulation were el-
₁₄₁₈ evated above randomly permuted data within a lag of $2.53 \pm 9.8 \times 10^{-3}$ consecutive trials
₁₄₁₉ (lower panel).

1420 **9.7 Supplemental Figure S3**



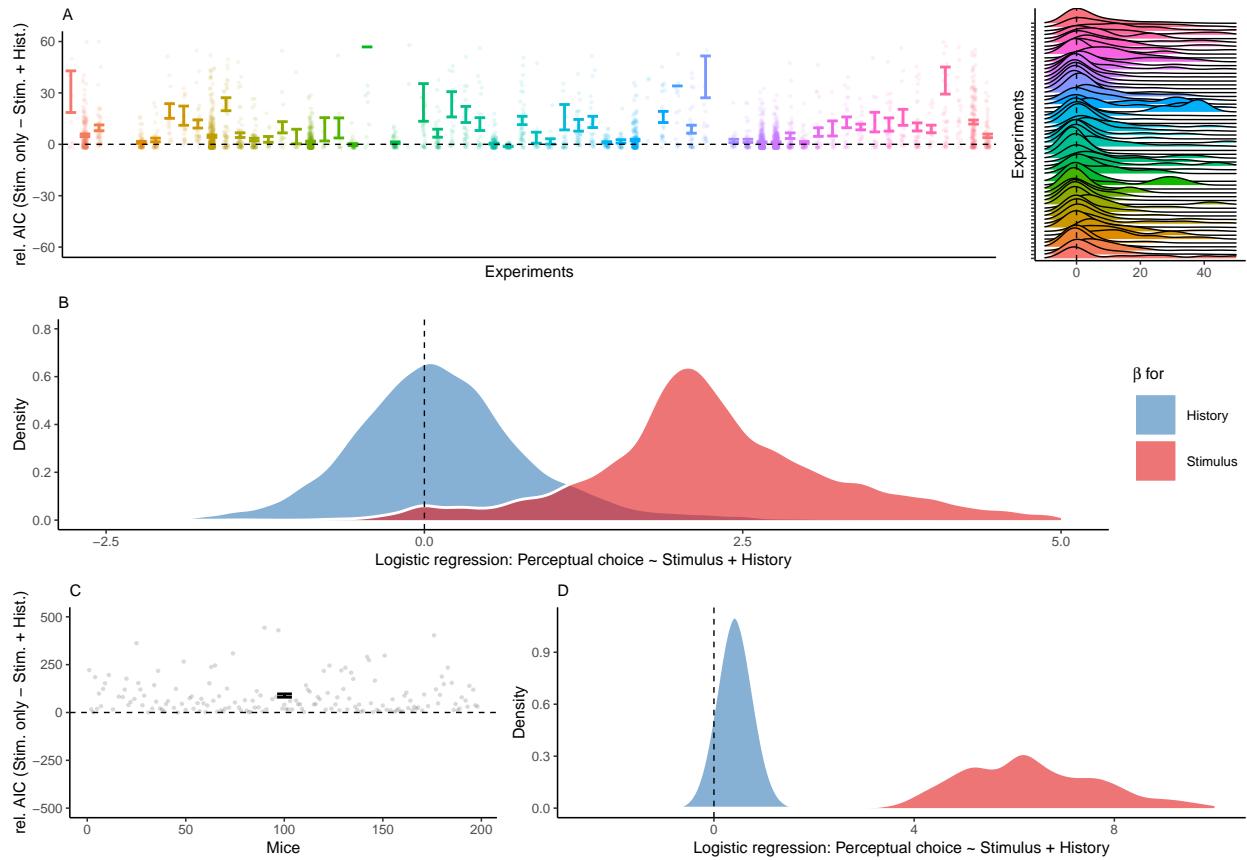
1422 **Supplemental Figure S3. Reproducing group-level autocorrelations using logistic
1423 regression.**

1424 A. As an alternative to group-level autocorrelation coefficients, we used trial-wise logistic
1425 regression to quantify serial dependencies in stimulus- and history-congruence. This analysis
1426 predicted stimulus- and history-congruence at the index trial (trial $t = 0$, vertical line)
1427 based on stimulus- and history-congruence at the 100 preceding trials. Mirroring the shape
1428 of the group-level autocorrelations, trial-wise regression coefficients (depicted as mean \pm
1429 SEM, dots mark trials with regression weights significantly greater than zero at $p < 0.05$)
1430 increased toward the index trial $t = 0$ for the human data.

1431 B. Following our results in human data, regression coefficients that predicted history-
1432 congruence at the index trial (trial $t = 0$, vertical line) increased exponentially for trials
1433 closer to the index trial in mice. In contrast to history-congruence, stimulus-congruence

¹⁴³⁴ showed a negative regression weight (or autocorrelation coefficient; Figure 3B) at trial -2.
¹⁴³⁵ This was due to the experimental design (see also the autocorrelations of difficulty and
¹⁴³⁶ external stimulation in Supplemental Figure S2C and D): When mice made errors at easy
¹⁴³⁷ trials (contrast $\geq 50\%$), the upcoming stimulus was shown at the same spatial location and
¹⁴³⁸ at high contrast. This increased the probability of stimulus-congruent perceptual choices
¹⁴³⁹ after stimulus-incongruent perceptual choices at easy trials, thereby creating a negative
¹⁴⁴⁰ regression weight (or autocorrelation coefficient) of stimulus-congruence at trial -2.

1441 **9.8 Supplemental Figure S4**



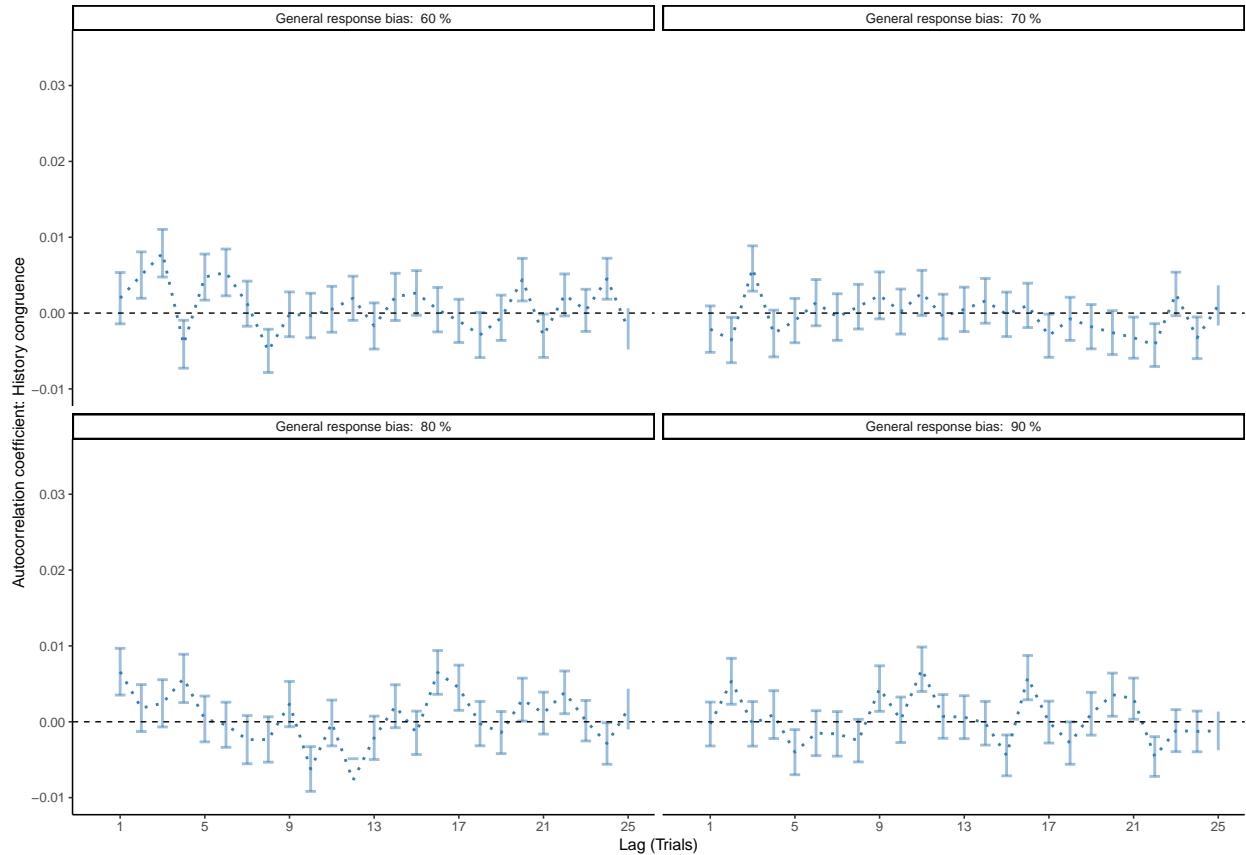
1442 **Supplemental Figure S4. History-congruence in logistic regression.**

1443 A. To ensure that perceptual history played a significant role in perception despite the ongoing stream of external information, we tested whether human perceptual decision-making was better explained by the combination of external and internal information or, alternatively, by external information alone. To this end, we compared AIC between logistic regression models that predicted trial-wise perceptual responses either by both current external sensory information and the preceding percept, or by external sensory information alone (values above zero indicate a superiority of the full model). With high consistency across the experiments selected from the Confidence Database, this model-comparison confirmed that perceptual history contributed significantly to perception (difference in AIC = 8.07 ± 0.53 , $T(57.22) = 4.1$, $p = 1.31 \times 10^{-4}$).

1444 B. Participant-wise regression coefficients amount to 0.18 ± 0.02 for the effect of perceptual

- ₁₄₅₅ history and 2.51 ± 0.03 for external sensory stimulation.
- ₁₄₅₆ C. In mice, an AIC-based model comparison indicated that perception was better explained
₁₄₅₇ by logistic regression models that predicted trial-wise perceptual responses based on both
₁₄₅₈ current external sensory information and the preceding percept (difference in AIC = 88.62
₁₄₅₉ ± 8.57 , $T(164) = -10.34$, $p = 1.29 \times 10^{-19}$).
- ₁₄₆₀ D. In mice, individual regression coefficients amounted to 0.42 ± 0.02 for the effect of per-
₁₄₆₁ ceptual history and 6.91 ± 0.21 for external sensory stimulation.

1462 **9.9 Supplemental Figure S5**



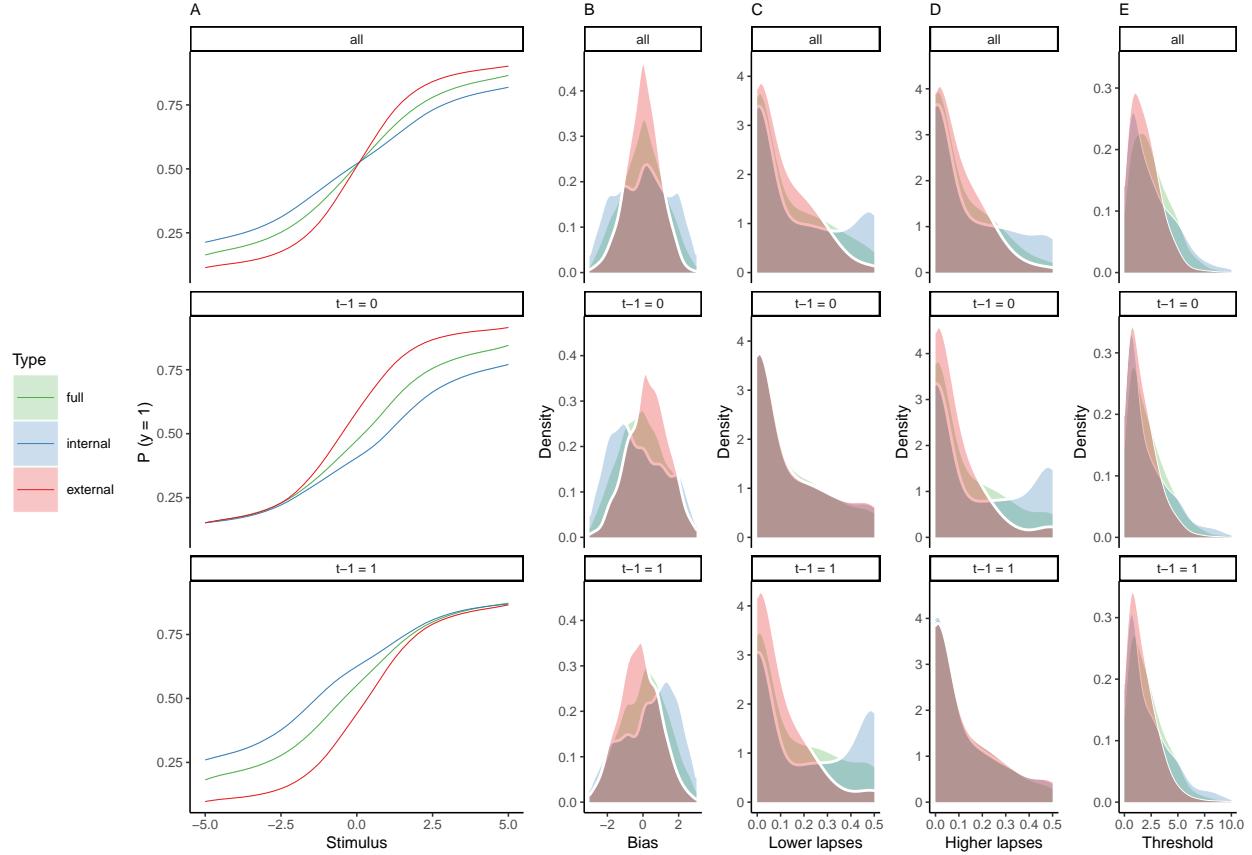
1463

1464 **Supplemental Figure S5. Correcting for general response biases.**

1465 Here, we ask whether the autocorrelation of history-congruence (as shown in Figure 2-3C)
1466 may be driven by general response biases (i.e., a general propensity to choose one of the
1467 two possible outcomes more frequently than the alternative). To this end, we generated
1468 sequences of 100 perceptual choices with general response biases ranging from 60 to 90%
1469 for 1000 simulated participants each. We then computed the autocorrelation of history-
1470 congruence for these simulated data. Crucially, we used the correction procedure that is
1471 applied to the autocorrelation curves shown in this manuscript: All reported autocorrelation
1472 coefficients are computed relative to the average autocorrelation coefficients obtained for
1473 100 iterations of randomly permuted trial sequences. The above simulation show that this
1474 correction procedure removes any potential contribution of general response biases to the
1475 autocorrelation of history-congruence. This indicates that the autocorrelation of history-

¹⁴⁷⁶ congruence (as shown in Figure 2-3C) is not driven by general response biases that were
¹⁴⁷⁷ present in the empirical data at a level of $58.71\% \pm 0.22\%$ in humans and $54.6\% \pm 0.3\%$ in
¹⁴⁷⁸ mice.

1479 **9.10 Supplemental Figure S6**



1480 **Supplemental Figure S6. Full and history-conditioned psychometric functions**

1481 **across modes in humans.**

1482 A. Here, we show average psychometric functions for the full dataset (upper panel) and
 1483 conditioned on perceptual history ($y_{t-1} = 1$ and $y_{t-1} = 0$; middle and lower panel) across
 1484 modes (green line) and for internal mode (blue line) and external mode (red line) separately.
 1485

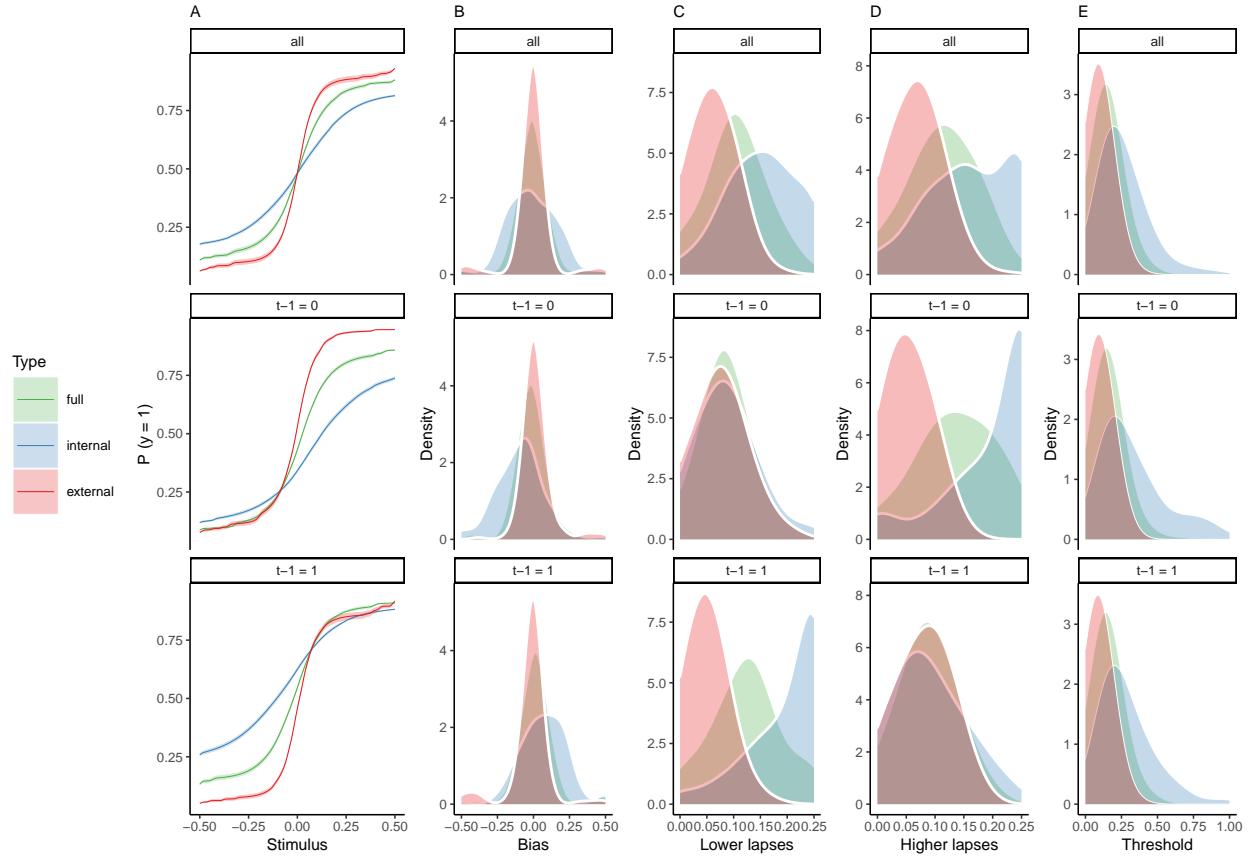
1486 B. Across the full dataset, biases μ were distributed around zero ($\beta_0 = 7.37 \times 10^{-3} \pm$
 1487 0.09, $T(36.8) = 0.08$, $p = 0.94$; upper panel), with larger absolute biases $|\mu|$ for internal
 1488 as compared to external mode ($\beta_0 = -0.62 \pm 0.07$, $T(45.62) = -8.38$, $p = 8.59 \times 10^{-11}$;
 1489 controlling for differences in lapses and thresholds). When conditioned on perceptual history,
 1490 we observed negative biases for $y_{t-1} = 0$ ($\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p = 3.64 \times 10^{-5}$;
 1491 middle panel) and positive biases for $y_{t-1} = 1$ ($\beta_0 = 0.56 \pm 0.12$, $T(43.39) = 4.6$, $p =$
 1492 3.64×10^{-5} ; lower panel).

₁₄₉₃ C. Lapse rates were higher in internal mode as compared to external mode ($\beta_0 = -0.05 \pm$
₁₄₉₄ 5.73×10^{-3} , $T(47.03) = -9.11$, $p = 5.94 \times 10^{-12}$; controlling for differences in biases and
₁₄₉₅ thresholds; see upper panel and subplot D). Importantly, the between-mode difference in
₁₄₉₆ lapses depended on perceptual history: We found no significant difference in lower lapses
₁₄₉₇ γ 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
₁₄₉₈ significant difference for $y_{t-1} = 1$ ($\beta_0 = -0.11 \pm 0.01$, $T(40.11) = -9.59$, $p = 6.14 \times 10^{-12}$;
₁₄₉₉ lower panel).

₁₅₀₀ D. Conversely, higher lapses δ were significantly increased for $y_{t-1} = 0$ ($\beta_0 = -0.1 \pm 9.58 \times$
₁₅₀₁ 10^{-3} , $T(36.87) = -10.16$, $p = 3.06 \times 10^{-12}$; middle panel), but not for $y_{t-1} = 1$ ($\beta_0 = 0.01$
₁₅₀₂ $\pm 7.74 \times 10^{-3}$, $T(33.66) = 1.58$, $p = 0.12$; lower panel).

₁₅₀₃ E. The thresholds t were larger in internal as compared to external mode ($\beta_0 = -1.77 \pm$
₁₅₀₄ 0.25 , $T(50.45) = -7.14$, $p = 3.48 \times 10^{-9}$; controlling for differences in biases and lapses)
₁₅₀₅ and were not modulated by perceptual history ($\beta_0 = 0.04 \pm 0.06$, $T(2.97 \times 10^3) = 0.73$, p
₁₅₀₆ $= 0.47$).

1507 **9.11 Supplemental Figure S7**



1508 **1509 Supplemental Figure S7. Full and history-conditioned psychometric functions**

1510 across modes in mice.

1511 A. Here, we show average psychometric functions for the full IBL dataset (upper panel) and
1512 conditioned on perceptual history ($y_{t-1} = 1$ and $y_{t-1} = 0$; middle and lower panel) across
1513 modes (green line) and for internal mode (blue line) and external mode (red line) separately.

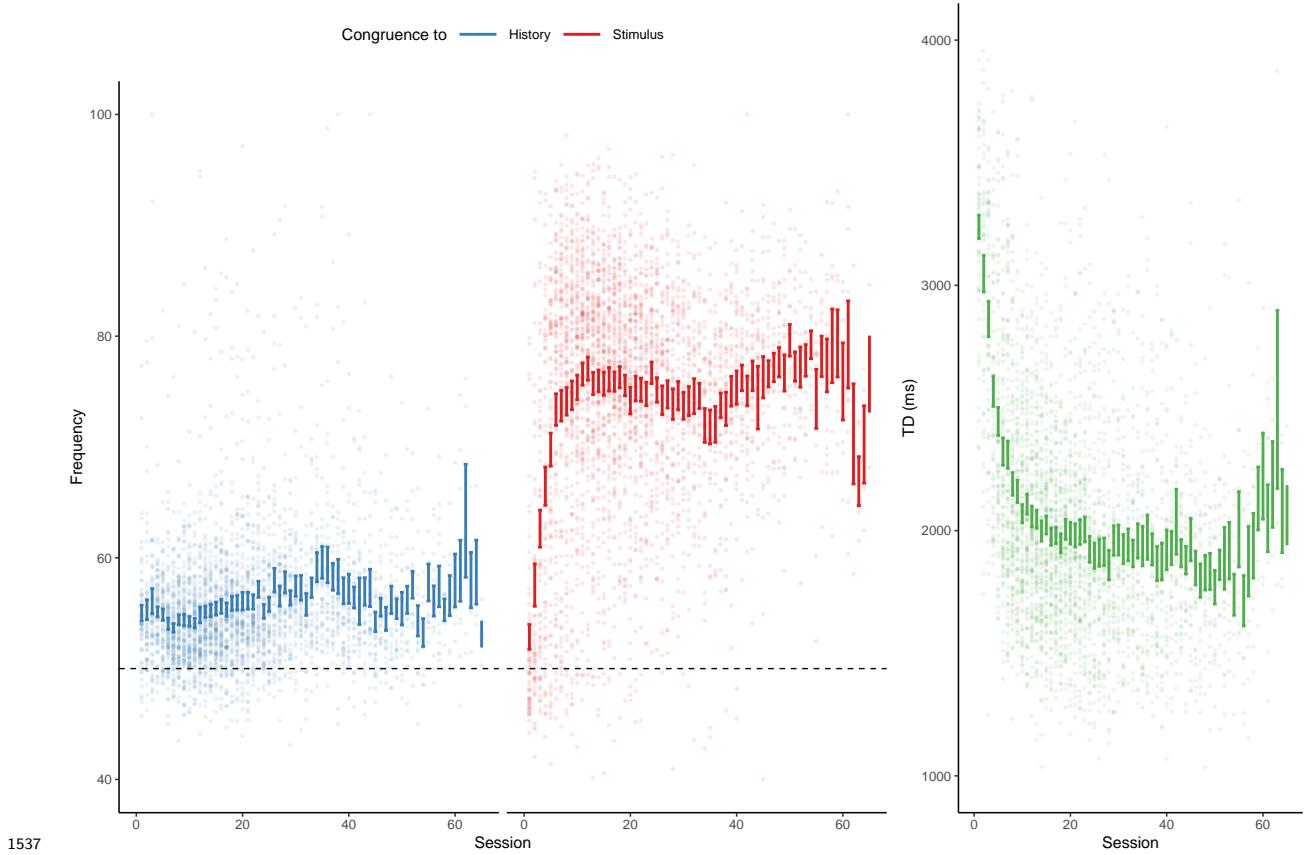
1514 B. Across the full dataset, biases μ were distributed around zero ($T(164) = 0.39$, $p = 0.69$;
1515 upper panel), with larger absolute biases $|\mu|$ for internal as compared to external mode ($\beta_0 =$
1516 -0.18 ± 0.03 , $T = -6.38$, $p = 1.77 \times 10^{-9}$; controlling for differences in lapses and thresholds).
1517 When conditioned on perceptual history, we observed negative biases for $y_{t-1} = 0$ ($T(164) = 1.91$, $p = 0.06$;
1518 = -1.99 , $p = 0.05$; middle panel) and positive biases for $y_{t-1} = 1$ ($T(164) = 1.91$, $p = 0.06$;
1519 lower panel).

1520 C. Lapse rates were higher in internal as compared to external mode ($\beta_0 = -0.11 \pm 4.39 \times$
1521 10^{-3} , $T = -24.8$, $p = 4.91 \times 10^{-57}$; controlling for differences in biases and thresholds; upper
1522 panel, see subplot D). For $y_{t-1} = 1$, the difference between internal and external mode was
1523 more pronounced for lower lapses γ ($T(164) = -18.24$, $p = 2.68 \times 10^{-41}$) as compared to
1524 higher lapses δ (see subplot D). In mice, lower lapses γ were significantly elevated during
1525 internal mode irrespective of the preceding perceptual choice (middle panel: lower lapses γ
1526 for $y_{t-1} = 0$; $T(164) = -2.5$, $p = 0.01$, lower panel: lower lapses γ for $y_{t-1} = 1$; $T(164) =$
1527 -32.44 , $p = 2.92 \times 10^{-73}$).

1528 D. For $y_{t-1} = 0$, the difference between internal and external mode was more pronounced
1529 for higher lapses δ ($T(164) = 21.44$, $p = 1.93 \times 10^{-49}$, see subplot C). Higher lapses were
1530 significantly elevated during internal mode irrespective of the preceding perceptual choice
1531 (middle panel: higher lapses δ for $y_{t-1} = 0$; $T(164) = -28.29$, $p = 5.62 \times 10^{-65}$ lower panel:
1532 higher lapses δ for $y_{t-1} = 1$; $T(164) = -2.65$, $p = 8.91 \times 10^{-3}$;).

1533 E. Thresholds t were higher in internal as compared to external mode ($\beta_0 = -0.28 \pm 0.04$,
1534 $T = -7.26$, $p = 1.53 \times 10^{-11}$; controlling for differences in biases and lapses) and were not
1535 modulated by perceptual history ($T(164) = 0.94$, $p = 0.35$).

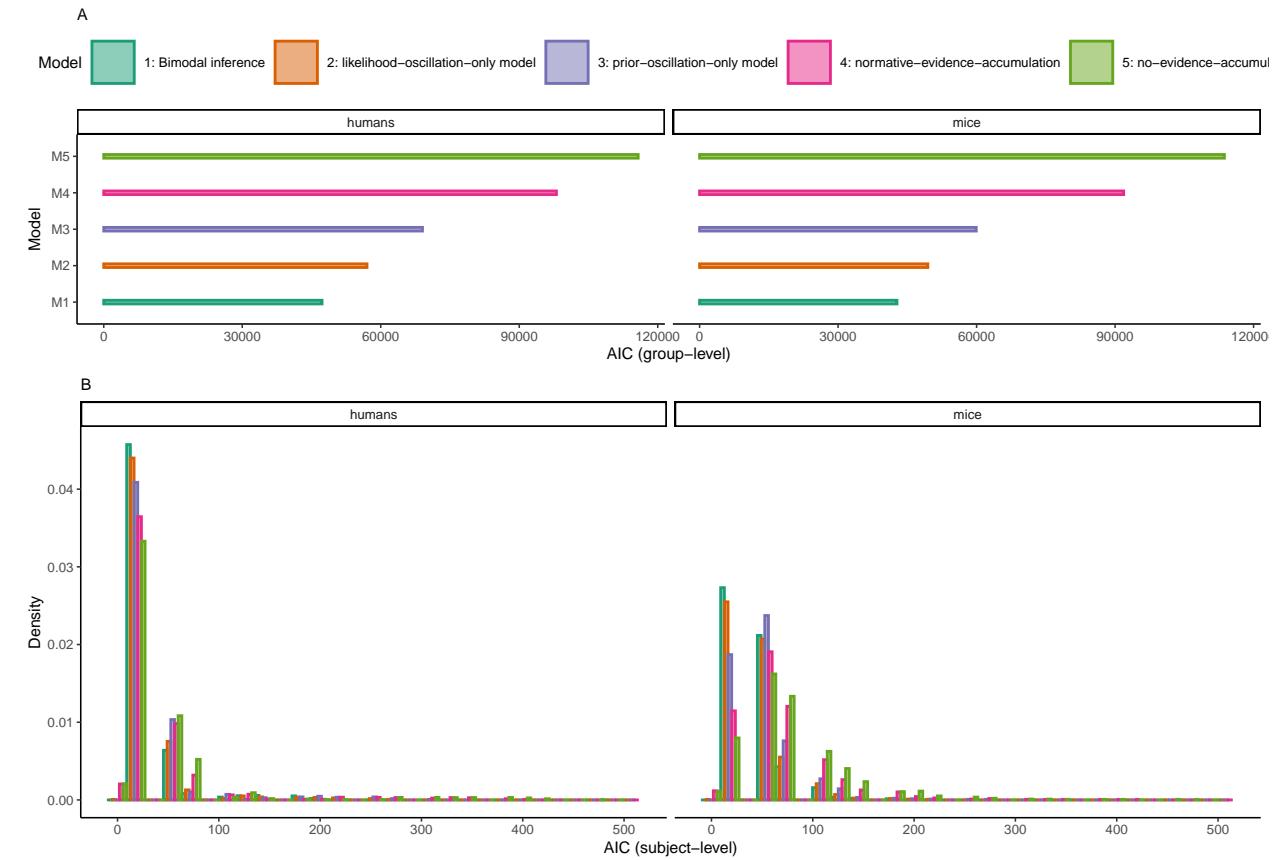
1536 **9.12 Supplemental Figure S8**



1538 **Supplemental Figure S8. History-/stimulus-congruence and TDs during training**
 1539 **of the basic task.**

1540 Here, we depict the progression of history- and stimulus-congruence (depicted in blue and
 1541 red, respectively; left panel) as well as TDs (in green; right panel) across training sessions in
 1542 mice that achieved proficiency (i.e., stimulus-congruence $\geq 80\%$) in the *basic* task of the IBL
 1543 dataset. We found that both history-congruent perceptual choices ($\beta = 0.13 \pm 4.67 \times 10^{-3}$,
 1544 $T(8.4 \times 10^3) = 27.04$, $p = 1.96 \times 10^{-154}$) and stimulus-congruent perceptual choices ($\beta =$
 1545 $0.34 \pm 7.13 \times 10^{-3}$, $T(8.51 \times 10^3) = 47.66$, $p = 0$) became more frequent with training. As
 1546 in humans, mice showed shorter TDs with increased exposure to the task ($\beta = -22.14 \pm$
 1547 17.06 , $T(1.14 \times 10^3) = -1.3$, $p = 0$).

1548 **9.13 Supplemental Figure S9**



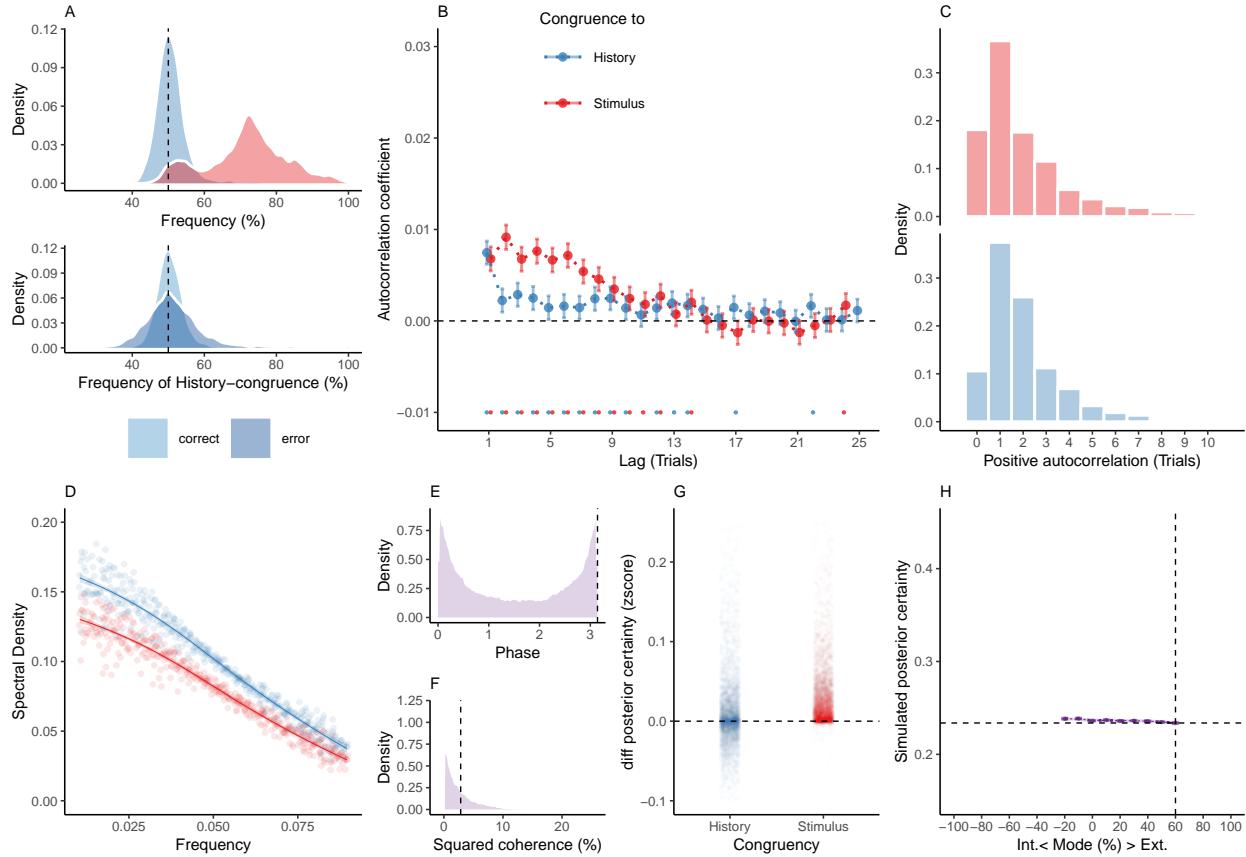
1549

1550 **Supplemental Figure S9. Comparison of the bimodal inference model against**
1551 **reduced control models.**

1552 **A. Group-level AIC.** The bimodal inference model (M1) achieved the lowest AIC
1553 across the full model space ($AIC_1 = 4.73 \times 10^4$ in humans and 4.28×10^4 in mice).
1554 Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model M3
1555 ($AIC_3 = 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated only oscillations
1556 of either likelihood or prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$ in humans
1557 and 9.19×10^4 in mice) lacked any oscillations of likelihood and prior precision
1558 and corresponded to the normative model proposed by Glaze et al.⁵¹. In model
1559 M5 ($AIC_5 = 1.16 \times 10^5$ in humans and 1.14×10^5 in mice), we furthermore removed
1560 the integration of information across trials, such that perception depended only
1561 in incoming sensory information.

1562 **B. Subject-level AIC.** Here, we show the distribution of AIC values at the
1563 subject-level. AIC for the bimodal inference model tended to be smaller than
1564 AIC for the comparator models (statistical comparison to the second-best model
1565 M2 in humans: $\beta = -1.81 \pm 0.27$, $T(5.07 \times 10^3) = -6.82$, $p = 1.02 \times 10^{-11}$; mice:
1566 $T(1.5 \times 10^3) = -6.28$, $p = 4.38 \times 10^{-10}$).

1567 **9.14 Supplemental Figure S10**



1568 **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_ψ 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 ζ .

1569 A. Similar to the full model M1 (Figure 1F and Figure 4), simulated perceptual choices
 1570 were stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted
 1571 to $50.76\% \pm 0.07\%$ of trials (in blue). As in the full model, the likelihood-oscillation-only
 1572 model showed a significant bias toward perceptual history $T(4.32 \times 10^3) = 10.29$, $p =$
 1573 1.54×10^{-24} ; upper panel). Similarly, history-congruent choices were more frequent at error
 1574 trials ($T(4.32 \times 10^3) = 9.71$, $p = 4.6 \times 10^{-22}$; lower panel).

1575 B. In the likelihood-oscillation-only model, we observed that the autocorrelation coeffi-

1581 cients for history-congruence were reduced below the autocorrelation coefficients of stimulus-
1582 congruence. This is an approximately five-fold reduction relative to the empirical results
1583 observed in humans (Figure 2B), where the autocorrelation of history-congruence was above
1584 the autocorrelation of stimulus-congruence. Moreover, in the reduced model shown here, the
1585 number of consecutive trials that showed significant autocorrelation of history-congruence
1586 was reduced to 11.

1587 C. In the likelihood-oscillation-only model, the number of consecutive trials at which true
1588 autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted
1589 data did not differ with respect to stimulus-congruence ($2.62 \pm 1.39 \times 10^{-3}$ trials; $T(4.32 \times$
1590 $10^3) = 1.85$, $p = 0.06$), but decreased with respect to history-congruence ($2.4 \pm 8.45 \times 10^{-4}$
1591 trials; $T(4.32 \times 10^3) = -15.26$, $p = 3.11 \times 10^{-51}$) relative to the full model.

1592 D. In the likelihood-oscillation-only model, the smoothed probabilities of stimulus- and
1593 history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant pro-**
1594 **cess with a 1/f power law**, i.e., at power densities that were inversely proportional to the
1595 frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.81 \pm 1.17 \times 10^{-3}$, $T(1.92 \times 10^5) =$
1596 -688.65 , $p = 0$; history-congruence: $\beta = -0.79 \pm 1.14 \times 10^{-3}$, $T(1.92 \times 10^5) = -698.13$, p
1597 $= 0$).

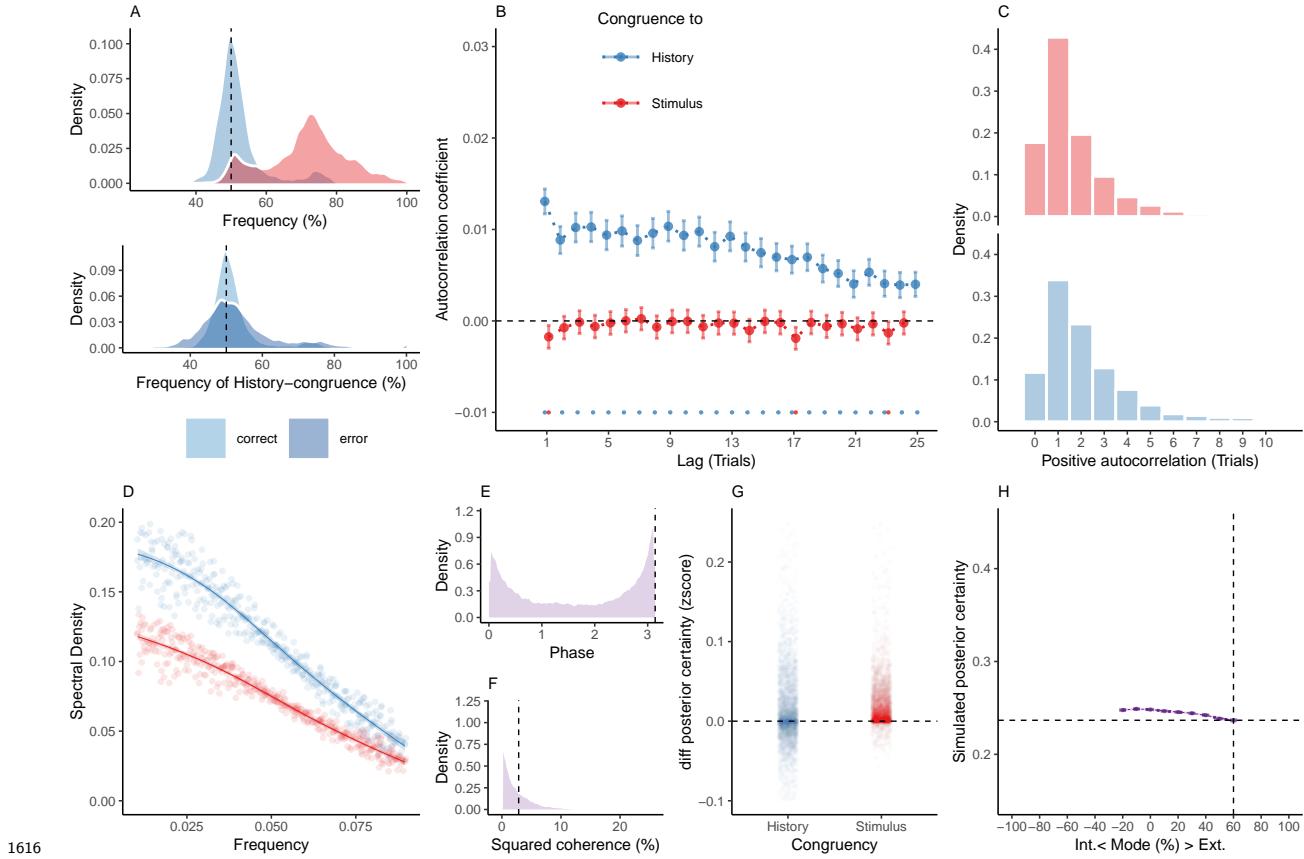
1598 E. In the likelihood-oscillation-only model, the distribution of phase shift between fluctua-
1599 tions in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by
1600 dotted line). In contrast to the full model, the dynamic probabilities of simulated stimulus-
1601 and history-congruence were positively correlated ($\beta = 2.7 \times 10^{-3} \pm 7.6 \times 10^{-4}$, $T(2.02 \times 10^6)$
1602 $= 3.55$, $p = 3.8 \times 10^{-4}$).

1603 F. In the likelihood-oscillation-only model, the average squared coherence between fluctua-
1604 tions in simulated stimulus- and history-congruence (black dotted line) was reduced in
1605 comparison to the full model ($T(3.51 \times 10^3) = -4.56$, $p = 5.27 \times 10^{-6}$) and amounted to 3.43
1606 $\pm 1.02 \times 10^{-3}\%$.

₁₆₀₇ G. Similar to the full bimodal inference model, confidence simulated from the likelihood-
₁₆₀₈ oscillation-only model was enhanced for stimulus-congruent choices ($\beta = 0.03 \pm 1.42 \times 10^{-4}$,
₁₆₀₉ $T(2.1 \times 10^6) = 191.78$, $p = 0$) and history-congruent choices ($\beta = 9.1 \times 10^{-3} \pm 1.25 \times 10^{-4}$,
₁₆₁₀ $T(2.1 \times 10^6) = 72.51$, $p = 0$).

₁₆₁₁ H. In the likelihood-oscillation-only model, the positive quadratic relationship between the
₁₆₁₂ mode of perceptual processing and confidence was markedly reduced in comparison to the full
₁₆₁₃ 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
₁₆₁₄ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1615 **9.15 Supplemental Figure S11**



1616 **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_ψ , frequency f , phase p and inverse decision temperature ζ .

1617 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1618 stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1619 $52.1\% \pm 0.11\%$ of trials (in blue). As in the full model, the prior-oscillation-only showed a
 1620 significant bias toward perceptual history $T(4.32 \times 10^3) = 18.34, p = 1.98 \times 10^{-72}$; upper
 1621 panel). Similarly, history-congruent choices were more frequent at error trials ($T(4.31 \times 10^3)$
 1622 $= 12.35, p = 1.88 \times 10^{-34}$; lower panel).

1623 B. In the prior-oscillation-only model, we did not observe any significant positive autocor-

₁₆₂₉ relation of stimulus-congruence , whereas the autocorrelation of history-congruence was pre-
₁₆₃₀ served.

₁₆₃₁ C. In the prior-oscillation-only model, the number of consecutive trials at which true au-
₁₆₃₂ tocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted
₁₆₃₃ data did was decreased with respect to stimulus-congruence relative to the full model ($1.8 \pm$
₁₆₃₄ 1.01×10^{-3} trials; $T(4.31 \times 10^3) = -6.48$, $p = 1.03 \times 10^{-10}$), but did not differ from the full
₁₆₃₅ model with respect to history-congruence ($4.25 \pm 1.84 \times 10^{-3}$ trials; $T(4.32 \times 10^3) = 0.07$,
₁₆₃₆ $p = 0.95$).

₁₆₃₇ D. In the prior-oscillation-only model, the smoothed probabilities of stimulus- and history-
₁₆₃₈ congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant process with a**
₁₆₃₉ **1/f power law**, i.e., at power densities that were inversely proportional to the frequency
₁₆₄₀ (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.78 \pm 1.11 \times 10^{-3}$, $T(1.92 \times 10^5) = -706.62$, p
₁₆₄₁ = 0; history-congruence: $\beta = -0.83 \pm 1.27 \times 10^{-3}$, $T(1.92 \times 10^5) = -651.6$, $p = 0$).

₁₆₄₂ E. In the prior-oscillation-only model, the distribution of phase shift between fluctuations
₁₆₄₃ in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by dotted
₁₆₄₄ line). Similar to the full model, the dynamic probabilities of simulated stimulus- and history-
₁₆₄₅ congruence were anti-correlated ($\beta = -0.03 \pm 8.61 \times 10^{-4}$, $T(2.12 \times 10^6) = -34.03$, $p =$
₁₆₄₆ 8.17×10^{-254}).

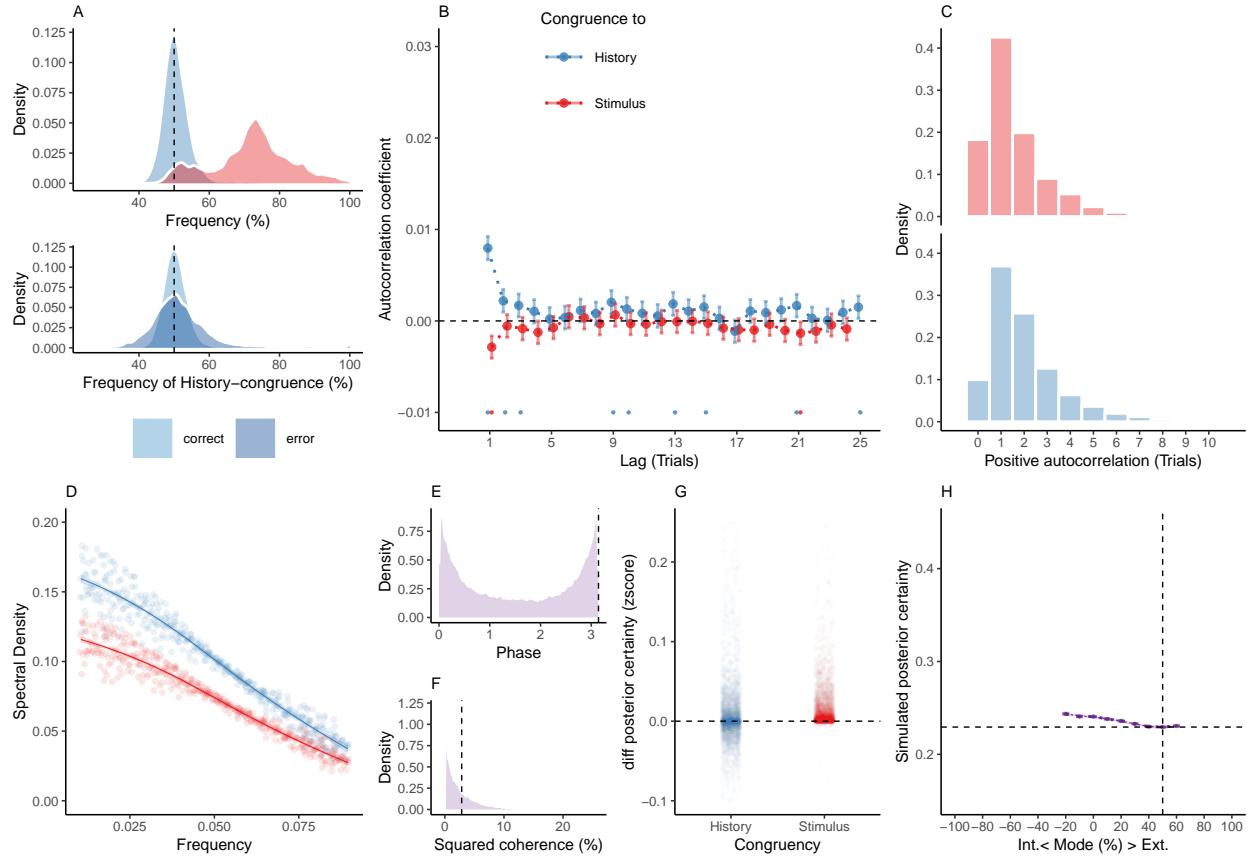
₁₆₄₇ F. In the prior-oscillation-only model, the average squared coherence between fluctuations in
₁₆₄₈ simulated stimulus- and history-congruence (black dotted line) was reduced in comparison to
₁₆₄₉ the full model ($T(3.54 \times 10^3) = -3.22$, $p = 1.28 \times 10^{-3}$) and amounted to $3.52 \pm 1.04 \times 10^{-3}\%$.

₁₆₅₀ G. Similar to the full bimodal inference model, confidence simulated from the prior-
₁₆₅₁ oscillation-only model was enhanced for stimulus-congruent choices ($\beta = 0.02 \pm 1.44 \times 10^{-4}$,
₁₆₅₂ $T(2.03 \times 10^6) = 128.53$, $p = 0$) and history-congruent choices ($\beta = 0.01 \pm 1.26 \times 10^{-4}$,
₁₆₅₃ $T(2.03 \times 10^6) = 88.24$, $p = 0$).

₁₆₅₄ H. In contrast to the full bimodal inference model, the prior-oscillation-only model did not

₁₆₅₅ yield a positive quadratic relationship between the mode of perceptual processing and con-
₁₆₅₆ fidence ($\beta_2 = -0.17 \pm 0.1$, $T(2.04 \times 10^6) = -1.66$, $p = 0.1$). The horizontal and vertical
₁₆₅₇ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1658 **9.16 Supplemental Figure S12**



1659 **1660 Supplemental Figure S12. Reduced Control Model M4: Normative evidence**

1661 **accumulation.** When simulating data for the *normative-evidence-accumulation model*, we
 1662 removed the oscillation from the likelihood and prior terms by setting the amplitudes a_{LLR}
 1663 and a_ψ to zero. Simulated data thus depended only on the participant-wise estimates for
 1664 hazard rate H and inverse decision temperature ζ .

1665 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1666 stimulus-congruent in $71.97\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1667 $50.73\% \pm 0.07\%$ of trials (in blue). As in the full model, the no-oscillation model showed
 1668 a significant bias toward perceptual history $T(4.32 \times 10^3) = 9.94$, $p = 4.88 \times 10^{-23}$; upper
 1669 panel). Similarly, history-congruent choices were more frequent at error trials ($T(4.31 \times 10^3)$
 1670 $= 10.59$, $p = 7.02 \times 10^{-26}$; lower panel).

1671 B. In the normative-evidence-accumulation model, we did not find significant autocorrela-

₁₆₇₂ tions for stimulus-congruence. Likewise, we did not observe any autocorrelation of history-
₁₆₇₃ congruence beyond the first three consecutive trials.

₁₆₇₄ C. In the normative-evidence-accumulation model, the number of consecutive trials at which
₁₆₇₅ true autocorrelation coefficients exceeded the autocorrelation coefficients for randomly per-
₁₆₇₆ muted data decreased with respect to both stimulus-congruence ($1.8 \pm 1.59 \times 10^{-3}$ trials;
₁₆₇₇ $T(4.31 \times 10^3) = -5.21$, $p = 2 \times 10^{-7}$) and history-congruence ($2.18 \pm 5.48 \times 10^{-4}$ trials;
₁₆₇₈ $T(4.32 \times 10^3) = -17.1$, $p = 1.75 \times 10^{-63}$) relative to the full model.

₁₆₇₉ D. In the normative-evidence-accumulation model, the smoothed probabilities of stimulus-
₁₆₈₀ and history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant pro-**
₁₆₈₁ **cess with a 1/f power law**, i.e., at power densities that were inversely proportional to the
₁₆₈₂ frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.78 \pm 1.1 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₆₈₃ -706.93 , $p = 0$; history-congruence: $\beta = -0.79 \pm 1.12 \times 10^{-3}$, $T(1.92 \times 10^5) = -702.46$, p
₁₆₈₄ $= 0$).

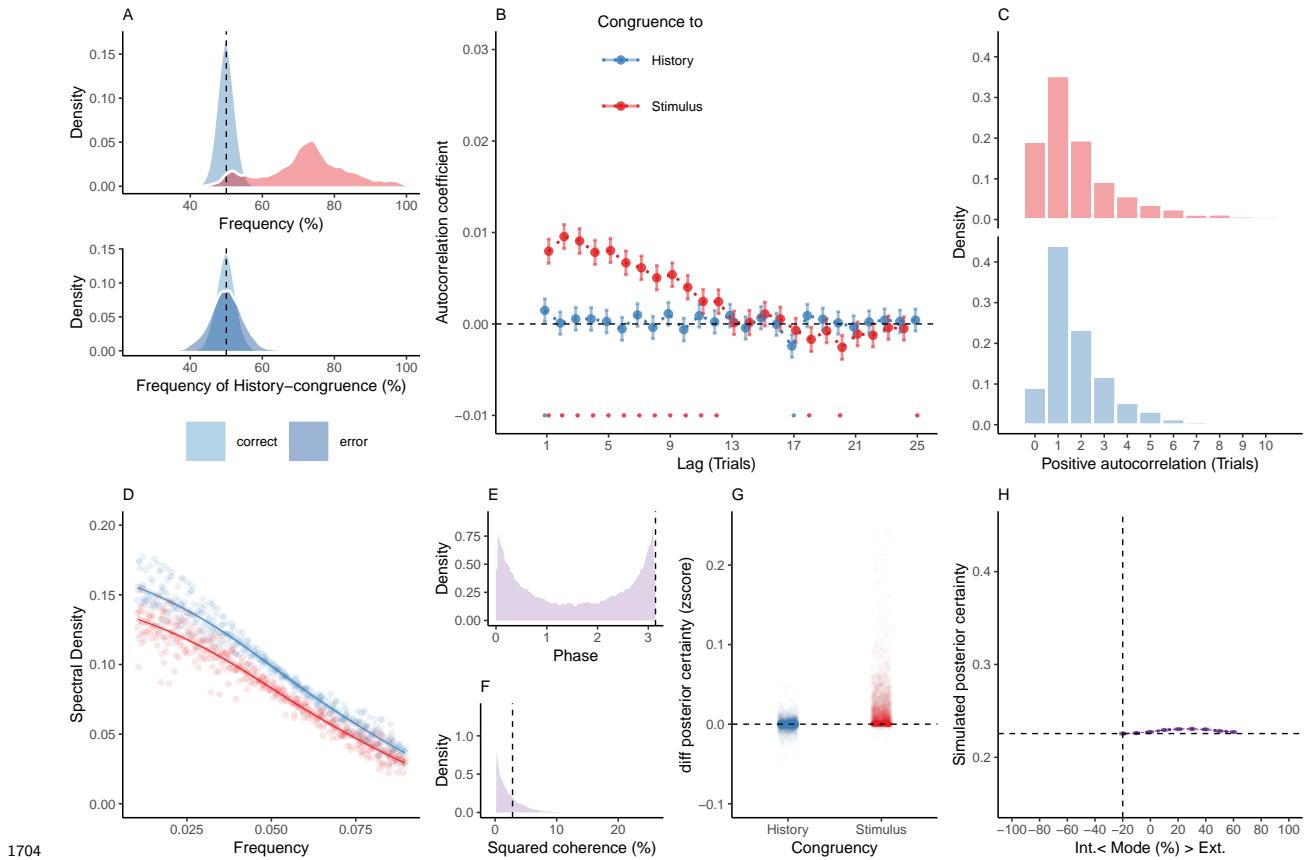
₁₆₈₅ E. In the normative-evidence-accumulation model, the distribution of phase shift between
₁₆₈₆ fluctuations in simulated stimulus- and history-congruence peaked at half a cycle (π denoted
₁₆₈₇ by dotted line). In contrast to the full model, the dynamic probabilities of simulated stimulus-
₁₆₈₈ and history-congruence were positively correlated ($\beta = 4.3 \times 10^{-3} \pm 7.97 \times 10^{-4}$, $T(1.98 \times 10^6)$
₁₆₈₉ $= 5.4$, $p = 6.59 \times 10^{-8}$).

₁₆₉₀ F. In the normative-evidence-accumulation model, the average squared coherence between
₁₆₉₁ fluctuations in simulated stimulus- and history-congruence (black dotted line) was reduced
₁₆₉₂ in comparison to the full model ($T(3.52 \times 10^3) = -6.27$, $p = 3.97 \times 10^{-10}$) and amounted to
₁₆₉₃ $3.26 \pm 8.88 \times 10^{-4}\%$.

₁₆₉₄ G. Similar to the full bimodal inference model, confidence simulated from the no-oscillation
₁₆₉₅ model was enhanced for stimulus-congruent choices ($\beta = 0.01 \pm 1.05 \times 10^{-4}$, $T(2.1 \times 10^6)$
₁₆₉₆ $= 139.17$, $p = 0$) and history-congruent choices ($\beta = 8.05 \times 10^{-3} \pm 9.2 \times 10^{-5}$, $T(2.1 \times 10^6)$
₁₆₉₇ $= 87.54$, $p = 0$).

₁₆₉₈ H. In the normative-evidence-accumulation model, the positive quadratic relationship be-
₁₆₉₉ tween the mode of perceptual processing and confidence was markedly reduced in compar-
₁₇₀₀ ison to the full model ($\beta_2 = 0.14 \pm 0.07$, $T(2.1 \times 10^6) = 1.95$, $p = 0.05$). The horizontal
₁₇₀₁ and vertical dotted lines indicate minimum posterior certainty and the associated mode,
₁₇₀₂ respectively.

1703 **9.17 Supplemental Figure S13**



1704 **1705 Supplemental Figure S13. Reduced Control Model M5: No accumulation of**

1706 **information across trials.** When simulating data for the *no-evidence-accumulation model*,
 1707 we removed the accumulation of information across trials by setting the Hazard rate H to
 1708 0.5. Simulated data thus depended only on the participant-wise estimates for the amplitudes
 1709 $a_{LLR/\psi}$, frequency f , phase p and inverse decision temperature ζ .

1710 A. Similar to the full model (Figure 1F and Figure 4), simulated perceptual choices were
 1711 stimulus-congruent in $72.14\% \pm 0.17\%$ of trials (in red). History-congruent amounted to
 1712 $49.89\% \pm 0.03\%$ of trials (in blue). In contrast to the full model, the no-accumulation model
 1713 showed a significant bias against perceptual history $T(4.32 \times 10^3) = -3.28$, $p = 1.06 \times 10^{-3}$;
 1714 upper panel). In contrast to the full model, there was no difference in the frequency of
 1715 history-congruent choices between correct and error trials ($T(4.31 \times 10^3) = 0.76$, $p = 0.44$;
 1716 lower panel).

₁₇₁₇ B. In the no-evidence-accumulation model, we found no significant autocorrelation of history-
₁₇₁₈ congruence beyond the first trial, whereas the autocorrelation of stimulus-congruence was
₁₇₁₉ preserved.

₁₇₂₀ C. In the no-evidence-accumulation model, the number of consecutive trials at which true
₁₇₂₁ autocorrelation coefficients exceeded the autocorrelation coefficients for randomly permuted
₁₇₂₂ data increased with respect to stimulus-congruence ($2.83 \pm 1.49 \times 10^{-3}$ trials; $T(4.31 \times 10^3) =$
₁₇₂₃ 3.45 , $p = 5.73 \times 10^{-4}$) and decreased with respect to history-congruence ($1.85 \pm 3.49 \times 10^{-4}$
₁₇₂₄ trials; $T(4.32 \times 10^3) = -19.37$, $p = 3.49 \times 10^{-80}$) relative to the full model.

₁₇₂₅ D. In the no-evidence-accumulation model, the smoothed probabilities of stimulus- and
₁₇₂₆ history-congruence (sliding windows of ± 5 trials) fluctuated as **a scale-invariant pro-**
₁₇₂₇ **cess with a 1/f power law**, i.e., at power densities that were inversely proportional to the
₁₇₂₈ frequency (power $\sim 1/f^\beta$; stimulus-congruence: $\beta = -0.82 \pm 1.2 \times 10^{-3}$, $T(1.92 \times 10^5) =$
₁₇₂₉ -681.98 , $p = 0$; history-congruence: $\beta = -0.78 \pm 1.11 \times 10^{-3}$, $T(1.92 \times 10^5) = -706.57$, p
₁₇₃₀ $= 0$).

₁₇₃₁ E. In the no-evidence-accumulation model, the distribution of phase shift between fluctua-
₁₇₃₂ tions in simulated stimulus- and history-congruence peaked at half a cycle (π denoted by
₁₇₃₃ dotted line). In contrast to the full model, the dynamic probabilities of simulated stimulus-
₁₇₃₄ and history-congruence were not significantly anti-correlated ($\beta = 6.39 \times 10^{-4} \pm 7.22 \times 10^{-4}$,
₁₇₃₅ $T(8.89 \times 10^5) = 0.89$, $p = 0.38$).

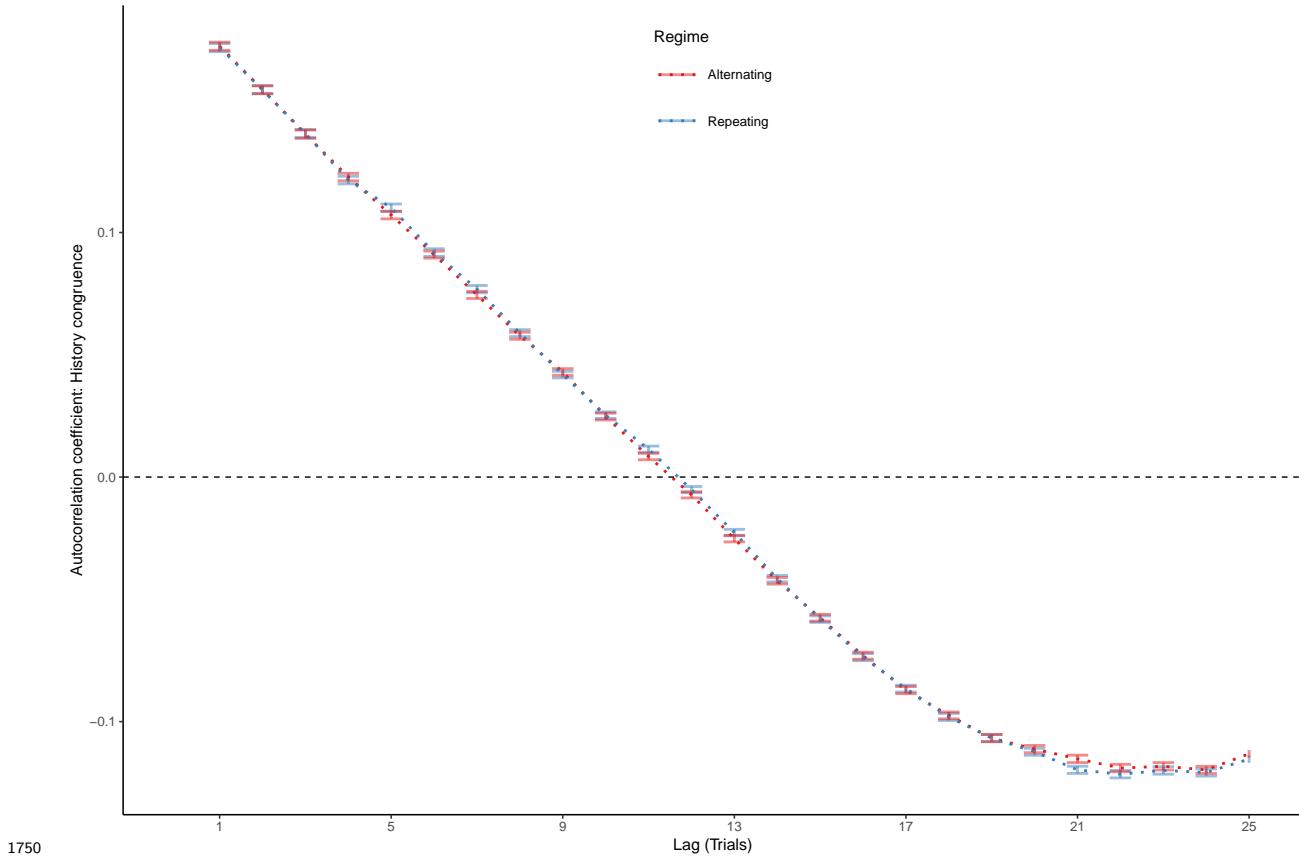
₁₇₃₆ F. In the no-evidence-accumulation model, the average squared coherence between fluctua-
₁₇₃₇ tions in simulated stimulus- and history-congruence (black dotted line) was reduced in
₁₇₃₈ comparison to the full model ($T(3.56 \times 10^3) = -9.96$, $p = 4.63 \times 10^{-23}$) and amounted to
₁₇₃₉ $2.8 \pm 7.29 \times 10^{-4}\%$.

₁₇₄₀ G. Similar to the full bimodal inference model, confidence simulated from the no-evidence-
₁₇₄₁ accumulation model was enhanced for stimulus-congruent choices ($\beta = 0.01 \pm 9.4 \times 10^{-5}$,
₁₇₄₂ $T(2.11 \times 10^6) = 158.1$, $p = 0$). In contrast to the full bimodal inference model, history-

₁₇₄₃ congruent choices were not characterized by enhanced confidence ($\beta = 8.78 \times 10^{-5} \pm 8.21 \times$
₁₇₄₄ 10^{-5} , $T(2.11 \times 10^6) = 1.07$, $p = 0.29$).

₁₇₄₅ H. In the no-evidence-accumulation model, the positive quadratic relationship between the
₁₇₄₆ mode of perceptual processing and confidence was markedly reduced in comparison to the
₁₇₄₇ full 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
₁₇₄₈ dotted lines indicate minimum posterior certainty and the associated mode, respectively.

1749 **9.18 Supplemental Figure S14**



1750 **Supplemental Figure S14. Autocorrelation of history-congruence of alternating
1751 and repeating biases.** Here, we simulate the autocorrelation of history-congruence in 10^3
1752 synthetic participants. In the repeating regime (blue), history-congruence fluctuated between
1753 50% and 80% (blue) in interleaved blocks (10 blocks per condition with a random duration
1754 between 15 and 30 trials). In the alternation regime (red), history-congruence fluctuated
1755 between 50% and 20%. The resulting autocorrelation curves for history-congruence overlap,
1756 indicating that our analysis is able to accommodate both repeating and alternating biases.
1757

₁₇₅₈ **9.19 Supplemental Table T1**

₁₇₅₉ **9.20 Supplemental Table T2**

1760 10 Response to Reviewers

1761 10.1 Reviewer 1:

1762 This was an interesting and thought-provoking submission. I note that it is
1763 a revision: I am therefore supposing that the authors have already responded
1764 to one round of reviewer comments and that you are potentially interested in
1765 publishing this work. In brief, I think there are many elements of this report that
1766 warrant publication; however, there are some parts that are less compelling and
1767 could be deferred to a subsequent paper. The paper is far too long and would
1768 benefit greatly from being streamlined. Furthermore, some of the modeling is
1769 overengineered and is difficult to follow. I have tried to suggest how the authors
1770 might improve the presentation of their work in my comments to authors.

1771 I enjoyed reading this long but thought-provoking report of fluctuations in the
1772 sensitivity to sensory evidence in perceptual decision-making tasks. There were
1773 some parts of this report that were compelling and interesting. Other parts were
1774 less convincing and difficult to understand. Overall, this paper is far too long.
1775 An analogy that might help here is that a dinner guest is very entertaining for the
1776 first hour or so - and then overstays their welcome; until you start wishing they
1777 would leave. Another analogy, which came to mind, was that the modeling—
1778 and its interpretation—was a bit autistic (i.e., lots of fascinating if questionable
1779 detail with a lack of central coherence).

1780 I think that both issues could be resolved by shortening the paper and removing
1781 (or, at least, greatly simplifying) the final simulation studies of metacognition.
1782 I try to unpack this suggestion in the following.

1783 We would like to thank Prof. Friston for the very insightful and helpful comments on our
1784 manuscript. We fully agree that our ideas about the computational function of between-mode

1785 fluctuations and the associated simulations may be presented in a more accessible form in
1786 a standalone paper. As we outlined in more detail below, we have streamlined our findings
1787 and rewrote the paper and reduced it's length by shortening the sections on computational
1788 modeling. We have also followed Prof. Friston's suggestion to interpret the effects of mode
1789 on RT and confidence in the context of predictive processing definitions of attention, namely
1790 the allocation of precision between prior and likelihood.

1791 **Major points:**

1792 **As I understand it, you have used publicly available data on perceptual decision-**
1793 **making to demonstrate slow fluctuations in the tendency to predicate perceptual**
1794 **decisions on the stimuli and on the history of recent decisions. You find scale-free**
1795 **fluctuations in this tendency — that are anti-correlated — and interpret this as**
1796 **fluctuations in the precision afforded sensory evidence, relative to prior beliefs.**
1797 **This interpretation is based upon a model of serial dependencies (parameterised**
1798 **with a hazard function).**

1799 **The stimulus and history (i.e., likelihood and prior) sensitivities are anti-**
1800 **correlated and both show scale free behavior. This is reproduced in men and**
1801 **mice. You then proceed to model this with periodic fluctuations in the precisions**
1802 **or weights applied to the likelihood and prior that are in anti-phase - and then**
1803 **estimate the parameters of the ensuing model. Finally, you then simulate the**
1804 **learning of the hazard parameter — and something called metacognition - to**
1805 **show that periodic fluctuations improve estimates of metacognition (based upon**
1806 **a Rescorla-Wagner model of learning). You motivate this by suggesting that**
1807 **the fluctuations in sensitivity are somehow necessary to elude circular inference**
1808 **and provide better estimates of precision.**

1809 **Note that I am reading the parameters omega_LL and omega_ as the preci-**
1810 **sion of the likelihood and prior, where the precision of the likelihood is called**

₁₈₁₁ sensory precision. This contrasts with your use of sensory precision, which seems
₁₈₁₂ to be attributed to a metacognitive construct M.

₁₈₁₃ As noted above, all of this is fascinating but there are too many moving parts
₁₈₁₄ that do not fit together comfortably. I will list a few examples:

₁₈₁₅ 10.1.1 Comment 1

₁₈₁₆ If, empirically, the fluctuations in sensitivity are scale-free with a 1/f power law,
₁₈₁₇ why did you elect to model fluctuations in precision as a periodic function with
₁₈₁₈ one unique timescale (i.e., f).?

₁₈₁₉ The reason for choosing a unique timescale f was to enable our model to depict the dominant
₁₈₂₀ timescale at which prior and likelihood precision are shifted against each other, giving rise
₁₈₂₁ to what constitutes between-mode fluctuations. We think that identifying this timescale is
₁₈₂₂ important for planning future experiments targeted at between-mode fluctuations and their
₁₈₂₃ manipulation by causal interventions (e.g., pharmacology or TMS). The posterior value
₁₈₂₄ for f lies at approximately $0.11 \text{ } 1/N_{\text{trials}}$ in both humans and mice. The value of f ap-
₁₈₂₅ proximately matches the transition probabilities between *engaged* and *disengaged* states in
₁₈₂₆ work assessing fluctuations in perceptual decision-making using Hidden Markov models (stay
₁₈₂₇ probabilities ranged between 0.94 and 0.98, see Ashwood et al., Nature Neuroscience 2022).
₁₈₂₈ Simulating from our model (Figure 4) replicates the 1/f feature of the empirical data. Please
₁₈₂₉ note that the individual trial is the smallest unit of *measurement* for these fluctuations, such
₁₈₃₀ that our analysis is limited by definition to frequencies below $1 \text{ } (1/N_{\text{trials}})$.

₁₈₃₁ We now provide a rationale for choosing one value for f - identifying the dominant timescale
₁₈₃₂ for fluctuations in mode - in the results section:

- ₁₈₃₃ • To allow for *bimodal inference*, i.e., alternating periods of internally- and
₁₈₃₄ externally-biased modes of perceptual processing that occur irrespective of
₁₈₃₅ the sequence of preceding experiences, we assumed that likelihood and prior

1836 vary in their influence on the perceptual decision according to fluctuations
 1837 governed by ω_{LLR} and ω_ψ . These anti-phase sine functions (defined by am-
 1838 plitudes $a_{LLR/\psi}$, frequency f and phase p) determine the precision afforded
 1839 to the likelihood and prior⁵³. The implicit anti-phase fluctuations are man-
 1840 dated by Bayes-optimal formulations in which inference depends only on the
 1841 relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴).
 1842 As such, ω_{LLR} and ω_ψ implement a hyperprior⁵⁵ in which the likelihood
 1843 and prior precisions are shifted against each other at a dominant timescale
 1844 defined by f^*

- 1845 • (...)The parameter f captures the dominant time scale at which likelihood
 1846 (amplitude humans: $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$; mice: $a_{LLR} = 0.39 \pm 1.08 \times 10^{-3}$
 1847 and prior precision (amplitude humans: $a_\psi = 1.44 \pm 5.27 \times 10^{-4}$; mice: $a_\psi =$
 1848 $1.71 \pm 7.15 \times 10^{-3}$ were shifted against each other and was estimated at 0.11
 1849 $\pm 1.68 \times 10^{-5} 1/N_{trials}$ and $0.11 \pm 1.63 \times 10^{-4} 1/N_{trials}$ in mice.
- 1850 • Table 2 (see response to Comment 22 by Reviewer 1) contains an additional definition
 1851 for all model parameters, including f .

1852 10.1.2 Comment 2

1853 At present, the estimates of meta-cognition (M) play the role of accumulated
 1854 estimates of (sensory or prior) precision. Why are these not used in your model
 1855 of perceptual decisions in Equation 2.

1856 In our model, the parameter α controls the encoding precision by governing the transfor-
 1857 mation from sensory stimuli to the log likelihood ratio (LLR) via the following equations (the
 1858 LLR ends up closer closer to zero when α is low):

$$u_t = \frac{1}{1 + \exp(-\alpha * s_t)} \quad (19)$$

$$LLR_t = \log\left(\frac{u_t}{1-u_t}\right) \quad (20)$$

1859 Our model simulations on the adaptive benefits of bimodal inference rest on the assumption
 1860 that α may change unpredictably. The construct M is a belief about α that may be useful
 1861 for, e.g., communicating the precision of sensory encoding to other cognitive domains or
 1862 agents. To our mind, α is a feature of low-level sensory encoding that cannot be modulated
 1863 by top-down beliefs such as M . This is why we did not include M in equation (2).

1864 **10.1.3 Comment 3**

1865 **Why do you assume that non-specific increases in attention and arousal will**
 1866 **increase reaction times? If one has very precise prior beliefs (and is not attending**
 1867 **to stimuli), would you not expect a decrease in reaction time?**

1868 Thanks a lot for pointing this out (see also the Comment below and Comment 6 by Reviewer
 1869 3). Both high prior and high likelihood precision lead to higher absolute values of the log
 1870 posterior ratio (reflecting certainty encoded by the decision variable), and thus faster RTs.
 1871 This is reflected empirically by RTs in humans (Figure 2) and to a lesser degree in mice
 1872 (Figure 3): RTs tended to be shorter for stronger biases toward both external and internal
 1873 mode. Our model, which incorporates (i), the accumulation of information across trials, and
 1874 (ii), fluctuations in the likelihood precision relative to the prior precision, recapitulates this
 1875 feature of the data, which is lost or greatly attenuated when eliminating process (i) and/or
 1876 (ii) (see model comparison and simulations below). Our data thus confirm the hypothesis
 1877 that both high prior and likelihood precision lead to faster RTs.

1878 In the previous version of the manuscript, we had included the relation between mode and
 1879 RTs and confidence primarily as a defensive analysis against the proposition that what we
 1880 call between-mode fluctuations is not a perceptual phenomenon, but occurs downstream of
 1881 perception. One may imagine that fluctuations in perceptual performance are not influenced

1882 by periods of relative increases in prior precision (which decrease performance in fully ran-
1883 domized designs), but by periods when participants do not attend to the task at all, i.e.,
1884 neither to sensory information nor to prior precision. We propose that the analyses of RTs
1885 and confidence can give some insight into whether such alternative mechanisms may be at
1886 play, as we would assume longer RTs and lower confidence if participants failed to attend to
1887 the task at all.

1888 That being said, we realize that, due to the potential non-linearity in their relation to arousal
1889 (see also Comment 6 by Reviewer 3), RTs and confidence cannot provide a definitive map
1890 of where fluctuations in mode are situated in relation to arousal. Such a delineation may
1891 potentially be provided by tracking of pupil size, response behavior or by neural data (e.g.,
1892 noise correlations of fluctuations in LFP). These data are not available for the studies in
1893 the Confidence Database, but were very recently published for the IBL database (after this
1894 manuscript was submitted). While we believe that this is beyond the scope of this manuscript,
1895 we will assess the relation of pupil diameter, motor behavior (turning of the response wheel)
1896 and LFPs to between-mode fluctuations in a future publication using the IBL dataset.

1897 In the light of the considerations above and our response to Comment 6 by Reviewer 3,
1898 we now refer to attention in the predictive processing sense. We now use the term “task
1899 engagement” instead of “on-task attention” to refer to situation in which participants may
1900 not attend to the task at all, e.g. due to low arousal or fatigue, and discuss these as alternative
1901 explanations for between-mode fluctuations. We have made three sets of changes to our
1902 manuscript:

1903 First, we present our results on the relation of mode to RT and Confidence in a more
1904 descriptive way, and do not use it as a strong defensive analysis against:

- 1905 • **The above results point to systematic fluctuations in the *decision variable*⁴⁴**
1906 **that determines perceptual choices, causing enhanced sensitivity to external**
1907 **stimulus information during external mode and increased biases toward pre-**

1908 ceding choices during internal mode. As such, fluctuations in mode should
1909 influence downstream aspects of behavior and cognition that operate on the
1910 perceptual decision variable⁴⁴. To test this hypothesis with respect to mo-
1911 tor behavior and metacognition, we asked how bimodal inference relates to
1912 response times (RTs) and confidence reports. (...)

1913 • (...). In sum, the above results indicate that reporting behavior and metacog-
1914 nition do not map linearly onto the mode of sensory processing. Rather, they
1915 suggest that slow fluctuations in the respective impact of external and in-
1916 ternal information are most likely to affect perception at an early level of
1917 sensory analysis^{46,47}. Such low-level processing may thus integrate percep-
1918 tual history with external inputs into a decision variable⁴⁴ that influences
1919 not only perceptual choices, but also the speed and confidence at which they
1920 are made.

1921 • In what follows, we probe alternative explanations for between-mode fluc-
1922 tuations, test for the existence of modes in mice, and propose a predictive
1923 processing model that explains fluctuations in mode ongoing shifts in the
1924 precision afforded to external sensory information relative to internal pre-
1925 dictions driven by perceptual history.

1926 Second, we have re-written our discussion of the quadratic relationship of mode to RTs and
1927 Confidence, focusing on predictive coding models attention:

1928 • As a functional explanation for bimodal inference, we propose that percep-
1929 tion temporarily disengages from internal predictions to form stable infer-
1930 ences about the statistical properties of the sensory environment. Between-
1931 mode fluctuations may thus elude circular inferences that occur when both
1932 the causes and the encoding of sensory stimuli are volatile^{19,57}. By the

1933 same token, we suggest that fluctuations in mode occur at the level of perceptual
1934 processing^{26,30,46,47}, and are not a passive phenomenon that is primarily driven by fac-
1935 tors situated up- or downstream of sensory analysis.

- 1936 • **How does attention relate to between-mode fluctuations?** According to pre-
1937 dictive processing, attention corresponds to the precision afforded to the
1938 probability distributions that underlie perceptual inference⁵³. From this
1939 perspective, fluctuations between external and internal mode can be under-
1940 stood as ongoing shifts in the attention afforded to either external sensory
1941 information (regulated via likelihood precision) or internal predictions (reg-
1942 ulated via precision precision). When the precision of either likelihood or
1943 prior increases, posterior precision increases, which leads to faster RTs and
1944 higher confidence. Therefore, when defined from the perspective of predi-
1945 ctive processing as the precision afforded to likelihood and prior⁵³, fluctua-
1946 tions in attention may provide a plausible explanation for the quadratic
1947 relationship of mode to RTs and confidence (Figure 2H and J; Figure 3I;
1948 **Figure 3I**).

1949 Third, we have added a more general discussion of our findings in the light of fluctuations
1950 in task engagement:

- 1951 • **Outside of the predictive processing field**, attention is often understood in
1952 the context of task engagement⁶³, which varies according to the availability
1953 of cognitive resources that are modulated by factors such as tonic arousal, fa-
1954 miliarity with the task, or fatigue⁶³. Our results suggest that internal mode
1955 processing cannot be completely reduced to intervals of low task engage-
1956 ment: In addition to shorter RTs and elevated confidence, choices during
1957 internal mode were not random or globally biased, but driven by percep-
1958 tual history (Supplemental Figures S6-7). Moreover, our computational

1959 model identified the dominant timescale of between-mode fluctuations at
1960 $0.11 \text{ } 1/N_{trials}$, which may be compatible with fluctuations in arousal⁶⁴, but
1961 is faster than to be expected for the development of task familiarity or fa-
1962 tigue.

- 1963 • However, in interpreting the impact of between-mode fluctuations on per-
1964 ceptual accuracy, speed of response and confidence, it is important to con-
1965 sider that global modulators such as tonic arousal are known to have non-
1966 linear effects on task performance⁶⁵: In perceptual tasks, performance seems
1967 so be highest during mid-level arousal, whereas low- and high-level arousal
1968 lead to reduced accuracy and slower responses⁶⁵. This contrasts with the
1969 effects of bimodal inference, where accuracy increases linearly as one moves
1970 from internal to external mode, and responses become faster at both ends
1971 of the mode spectrum.
- 1972 • Of note, high phasic arousal has been shown to suppress multi-domain bi-
1973 ases in decision-making in humans and mice^{66–68}, including the biases toward
1974 perceptual history²⁸ that we implicate in internal mode processing. The in-
1975 crease in response speed and history congruence over time (Supplemental
1976 Section 9.4) may argue against insufficient training as an alternative expla-
1977 nation for internal mode processing, but may also taken as a sign of waning
1978 arousal. The multiple mechanistic mappings to RTs and confidence there-
1979 fore warrant more direct measures of arousal (such as pupil size^{28,65,66,68–70},
1980 motor behavior^{69,70}, or neural data⁷¹) to better delineate bimodal inference
1981 from fluctuations in global modulators of task performance.

1982 **10.1.4 Comment 4**

1983 In the predictive processing literature, attention is thought to correspond to
1984 fluctuations in sensory and prior precision. Why did you then consider attention

1985 **as some additional or unrelated confound?**

1986 This point is closely related to the comment above. We realize that, in the predictive coding
1987 field, attention is equated with the precision of probability distributions that contribute to
1988 the perceptual decision, such that an observer can attend strongly to sensory information
1989 (high likelihood precision) or to internal predictions derived from the sequence of preced-
1990 ing percepts (high prior precision). Therefore, when following the above predictive coding
1991 definition, fluctuations in attention can be equated with fluctuations in mode.

1992 However, we feel that outside of the predictive coding field, attention is not always conceived
1993 in that way, such that low attention is often considered as low engagement with the task,
1994 i.e., relating to low likelihood and low prior precision in the predictive coding sense. It is
1995 against these caveats that our control analysis (based on psychometric functions, training
1996 effects, RTs and confidence) defend our conclusions on bimodal inference.

1997 We now provide a more nuanced interpretation of our findings of RTs and confidence in
1998 relation to attention, with a specific focus on predictive coding and precision. We hope that
1999 our responses to the comment above resolves the points raised in this comment.

2000 **10.1.5 Comment 5**

2001 **What licences the assumption that “agents depend upon internal confidence
2002 signals” in the absence of feedback?**

2003 In the absence of feedback, observers can only rely on internal estimates of performance to
2004 guide updates to their model of the reliability of their sensory apparatus (inferences about
2005 M). Previous work (e.g. Guggenmos et al., Elife 2106, <https://doi.org/10.7554/eLife.13388>)
2006 has shown that confidence signals can provide signals that drive perceptual learning in the
2007 absence of feedback. This has motivated our model simulation on the adaptive benefits of
2008 bimodal inference for metacognition, where the learning signal ϵ_M drives inferences about
2009 M :

$$\epsilon_M = (1 - |y_t - P(y_t = 1)|) - M_t \quad (21)$$

2010 **10.1.6 Comment 6**

2011 **And what licences the assumption that internal confidence feedback corresponds**
2012 **to “the absolute of the posterior log ratio” (did you mean the log of the posterior**
2013 **ratio)?**

2014 We mean the absolute of the log of the posterior ratio. Following first order models (see
2015 e.g., Fleming & Daw, Self-evaluation of decision-making: A general Bayesian framework for
2016 metacognitive computation, Psychol. Rev. 2017, <https://doi.org/10.1037/rev0000045>), the
2017 perceptual decision and the confidence report rely on the posterior. The distance of the log
2018 of the posterior ratio L_t from zero becomes a measure of decision-certainty or confidence.

2019 **10.1.7 Comment 7**

2020 **I got a bit lost here when you say that “the precision of sensory coding M a**
2021 **function of u_t. This is largely because I couldn’t find a definition of u_t.**

2022 We apologize for this lack of clarity. In the model simulations on the adaptive benefits of
2023 bimodal inference, we generated stimuli s_t from a Bernoulli-distribution with $p = q = 0.5$.
2024 The value of u_t was then defined via equation (22), following our modeling of the human
2025 data:

$$u_t = \frac{1}{1 + \exp(-\alpha * (s_t - 0.5))} \quad (22)$$

2026 **10.1.8 Comment 8**

2027 **What licences an application of Rescorla-Wagner to learning the parameters (as**
2028 **in Equation 11) and, learning sensory precision as described by M_T (Equation**

2029 **13). Are you moving from a Bayesian framework to a reinforcement learning**
2030 **framework?**

2031 We would like to thank the reviewer for pointing out this inconsistency. We have chosen the
2032 Rescorla-Wagner learning rule for simplicity: In our model, the speed of learning about H
2033 and M varies according to the current mode of perceptual processing and a constant learning
2034 rate:

$$H'_t = H'_{t-1} + \beta_H * \omega_{LLR} * \epsilon_H \quad (23)$$

$$M'_t = M'_{t-1} + \beta_M * \omega_{LLR} * \epsilon_M \quad (24)$$

2035 Allowing the learning rate itself to vary as a function of preceding experiences would add
2036 an additional level of complexity that we sought to omit in this analysis. However, we fully
2037 agree that choosing a Bayesian framework (e.g., a three-level HGF) would indeed be more
2038 consistent.

2039 **10.1.9 Comment 9**

2040 **I am sure you have answers to these questions - but with each new question**
2041 **the reader is left more and more skeptical that there is a coherent story behind**
2042 **your analyses. It would have been more convincing had you just committed to**
2043 **a Bayesian filter and made your points using one update scheme, under ideal**
2044 **Bayesian observer assumptions.**

2045 **Unlike your piecemeal scheme, things like the hierarchical Gaussian filter esti-**
2046 **mates the sensory and prior decisions explicitly and these estimates underwrite**
2047 **posterior inference. In your scheme, the sensory precision M appears to have no**
2048 **influence on perceptual inference (which is why, presumably you call it metacog-**

2049 nition). The problem with this is that your motivation for systematic fluctuations
2050 in precision is weakened. This is because improved metacognition does not
2051 improve perception — it only improves the perception of perception.

2052 In light of the above, can I suggest that you remove Section 5.8 and use your
2053 model in the preceding section to endorse your hypothesis along the following
2054 lines:

2055 “In summary, we hypothesized that subjects have certain hyperpriors that are
2056 apt for accommodating fluctuations in the predictability of their environment;
2057 i.e., people believe that their world is inherently volatile. This means that to be
2058 Bayes optimal it is necessary to periodically re-evaluate posterior beliefs about
2059 model parameters. One way to do this is to periodically suspend the precision of
2060 prior beliefs and increase the precision afforded to sensory evidence that updates
2061 (Bayesian) beliefs about model parameters. The empirical evidence above sug-
2062 gests that the timescale of this periodic scheduling of evidence accumulation may
2063 be scale-invariant. This means that there may exist a timescale of periodic fluc-
2064 tuations in precision over every window or length of perceptual decision-making.
2065 In what follows, we model perceptual decisions under a generative model (based
2066 upon a hazard function to model historical or serial dependencies) with, a peri-
2067 odic fluctuation in the precision of sensory evidence relative to prior beliefs at a
2068 particular timescale. Remarkably—using Bayesian model comparison—we find
2069 that a model with fluctuating precisions has much greater evidence, relative to
2070 a model in the absence of fluctuating precisions. Furthermore, we were able to
2071 quantify the dominant timescale of periodic fluctuations; appropriate for these
2072 kinds of paradigm.”

2073 Note, again, I am reading your ω_{LLR} and ω_{prior} as precisions and that
2074 the periodic modulation is the hyperprior that you are characterizing—and have

2075 discovered.

2076 We would like to thank Prof. Friston for these very helpful and precise suggestions. In brief,
2077 we now provide a quantitative assessment of model space based on AIC (i) and have followed
2078 the suggestion of omitting section 5.8 (ii).

2079 In addition to the qualitative assessment of our models in the initial version of our manuscript,
2080 we have conducted a formal model comparison (i). Following the model comparisons in other
2081 sections of the manuscript, we based the model comparison on AIC values. We furthermore
2082 show that the winning *bimodal inference model* predicts the out-of-training variables (RT and
2083 confidence) and use simulations from posterior model parameters to show that, in contrast
2084 to reduced models, the bimodal inference model neither over- nor underfits the empirical
2085 data. We have added a description of our model comparison to the Method section:

2086 • We validated the bimodal inference model in three steps: a formal model
2087 comparison to reduced models based on AIC (Figure 1F-G; Supplemen-
2088 tal Figure S9), the prediction of within-training (stimulus- and history-
2089 congruence) as well as out-of-training variables (RT and confidence), and
2090 a qualitative reproduction of the empirical data from model simulations
2091 based on estimated parameters (Figure 4).

- 2092 • Model comparison. We assessed the following model space based on AIC:
2093 • The full *bimodal inference model* (M1; Figure 1F) incorporates the influ-
2094 ence of sensory information according to the parameter α (likelihood); the
2095 integration of evidence across trials according to the parameter H (prior);
2096 anti-phase oscillations in between likelihood and prior precision according
2097 to ω_{LLR} and ω_ψ with parameters a_{LLR} (amplitude likelihood fluctuation), a_ψ
2098 (amplitude prior fluctuation), f (frequency) and p (phase).
2099 • The *likelihood-oscillation-only model* (M2; Figure 1G) incorporates the in-

fluence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior); oscillations in likelihood precision according to ω_{LLR} with parameters a_{LLR} (amplitude likelihood fluctuation), f (frequency) and p (phase).

- The *prior-oscillation-only model* (M3; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior); oscillations in the prior precision according to ω_ψ with parameters a_ψ (amplitude prior fluctuation), f (frequency) and p (phase). Please note that all models M1-3 lead to shifts in the relative precision of likelihood and prior.
- The *normative-evidence-accumulation* (M4; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood); the integration of evidence across trials according to parameter H (prior), There are no additional oscillations. Model M4 thus corresponds to the model proposed by Glaze et al. and captures normative evidence accumulation in unpredictable environments using a Bayesian update scheme⁵¹. The comparison against M4 tests the null hypothesis that fluctuations in mode emerge from a normative Bayesian model without the ad-hoc addition of oscillations as in models M1-3.
- The *no-evidence-accumulation* (M5; Figure 1G) incorporates the influence of sensory information according to parameter α (likelihood). The model lacks integration of evidence across trials (flat prior) and oscillations. The comparison against M5 tests the null hypothesis that observers do not use prior information derived from serial dependency in perception.
- Prediction of within-training and out-of-training variables. To validate our model, we correlated individual posterior parameter estimates with the re-

2126 spective conventional variables. As a sanity check, we tested (i), whether the
2127 estimated hazard rate H correlated negatively with the frequency of history-
2128 congruent choices and, (ii), whether the estimated sensitivity to sensory in-
2129 formation α correlated positively with the frequency of stimulus-congruent
2130 choices. In addition, we tested whether the posterior decision certainty (i.e..
2131 the absolute of the log posterior ratio) correlated negatively with RTs and
2132 positively with confidence. This allowed us to assess whether our model
2133 could explain aspects of the data it was not fitted to (i.e., RTs and confi-
2134 dence).

- 2135 • **Simulations.** Finally, we used simulations (Figure 4, Supplemental Figures
2136 S10-13) to show that all model components, including the anti-phase os-
2137 cillations governed by a_ψ , a_{LLR} , f and p , were necessary for our model to
2138 reproduce the characteristics of the empirical data. This enabled us to assess
2139 over- or under-fitting in the bimodal inference model and all reduced mod-
2140 els M2-M5. We used the posterior model parameters observed for humans
2141 (H , α , a_ψ , a_{LLR} , f and ζ) to define individual parameters for simulation in
2142 4317 simulated participants (i.e., equivalent to the number of human par-
2143 ticipants). For each participant, the number of simulated trials was drawn
2144 at random between 300 to 700. Inputs s were drawn at random for each
2145 trial, such that the sequence of inputs to the simulation did not contain
2146 any systematic seriality. Noisy observations u were generated by applying
2147 the posterior parameter α to inputs s , thus generating stimulus-congruent
2148 choices in $71.36 \pm 2.6 \times 10^{-3}\%$ of trials. Choices were simulated based on
2149 the trial-wise choice probabilities y_p obtained from our model. Simulated
2150 data were analyzed in analogy to the human and mouse data. As a substi-
2151 tute of subjective confidence, we computed the absolute of the trial-wise log
2152 posterior ratio $|L|$ (i.e., the posterior decision certainty).

2153 We have also added a graphical depiction of the model space to Figure 1 (subpanels F and
2154 G):

- 2155 • F. The bimodal inference model (M1) explains fluctuations between
2156 externally- and externally-biased modes (left panel) by two interacting
2157 factors: a normative accumulation of evidence according to parameters H
2158 (middle panel), and anti-phase oscillations in the precision terms ω_{LLR} and
2159 ω_ψ (right panel).
- 2160 • G. The control models M2-M5 were constructed by successively remov-
2161 ing the anti-phase oscillations and the integration of information from
2162 the bimodal inference model. Please note that the normative-evidence-
2163 accumulation-model (M4) corresponds to the model proposed by Glaze et
2164 al.⁵¹. In the no-evidence-accumulation model (M5), perceptual decisions
2165 depend only on likelihood information (flat priors).

2166 The formal model comparison yielded clear evidence for a superiority of the bimodal inference
2167 model, in particular over the normative Bayesian model of evidence accumulation. The model
2168 successfully predicted both within-training variables (as a sanity-check) and out-of-training
2169 variables. Simulations from posterior model parameters closely followed the empirical data
2170 (Figure 4), which was not the case for reduced models (Supplemental Figures S10-13). We
2171 summarize these findings in the Results section and have added a Supplemental Figure S9
2172 to show the distribution of observer-level AIC at the session-level (see below):

- 2173 • We used a maximum likelihood procedure to fit the bimodal inference model
2174 (M1, Figure 1F) to the behavioral data from the Confidence database²⁰ and
2175 the IBL database²¹, optimizing the parameters α , H , ω_{LLR} , ω_ψ , f and
2176 p (see Methods for details and Supplemental Table T2 for a summary of
2177 the parameters of the bimodal inference model). We validated our model

2178 in three steps: First, to show that bimodal inference does not emerge spont-
2179aneously in normative Bayesian models of evidence accumulation, but re-
2180quires the ad-hoc addition of anti-phase oscillations in prior and likelihood
2181precision, we compared the bimodal inference model to four control models
2182(M2-5, Figure 1G). In these models, we successively removed the anti-phase
2183oscillations (M2-M4) and the integration of information across trials (M5)
2184from the bimodal inference model and performed a model comparison based
2185on AIC.

- 2186 • Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model
2187 M3 ($AIC_3 = 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated only
2188 oscillations of either likelihood or prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$
2189 in humans and 9.19×10^4 in mice) lacked any oscillations of likelihood and
2190 prior precision and corresponded to the normative model proposed by Glaze
2191 et al.⁵¹. In model M5 ($AIC_4 = 1.16 \times 10^5$ in humans and 1.14×10^5 in mice), we
2192 furthermore removed the integration of information across trials, such that
2193 perception depended only in incoming sensory information (Figure 1G).
- 2194 • The bimodal inference model achieved the lowest AIC across the full model
2195 space ($AIC_1 = 4.73 \times 10^4$ in humans and 4.28×10^4 in mice) and was clearly
2196 superior to the normative Bayesian model of evidence accumulation (δ_{AIC}
2197 $= -5.08 \times 10^4$ in humans and -4.91×10^4 in mice; Supplemental Figure S9).
- 2198 • As a second validation of the bimodal inference model, we tested whether
2199 the posterior model predicted within-training and out-of-training variables.
2200 The bimodal inference model characterizes each subject by a sensitivity
2201 parameter α (humans: $\alpha = 0.5 \pm 1.12 \times 10^{-4}$; mice: $\alpha = 1.06 \pm 2.88 \times 10^{-3}$)
2202 that captures how strongly perception is driven by the available sensory
2203 information, and a hazard rate parameter H (humans: $H = 0.45 \pm 4.8 \times 10^{-5}$;

2204 mice: $H = 0.46 \pm 2.97 \times 10^{-4}$) that controls how heavily perception is biased
2205 by perceptual history. The parameter f captures the dominant time scale at
2206 which likelihood (amplitude humans: $a_{LLR} = 0.5 \pm 2.02 \times 10^{-4}$; mice: a_{LLR}
2207 = $0.39 \pm 1.08 \times 10^{-3}$) and prior precision (amplitude humans: $a_\psi = 1.44 \pm$
2208 5.27×10^{-4} ; mice: $a_\psi = 1.71 \pm 7.15 \times 10^{-3}$) fluctuated and was estimated at
2209 $0.11 \pm 1.68 \times 10^{-5}$ $1/N_{trials}$ and $0.11 \pm 1.63 \times 10^{-4}$ $1/N_{trials}$ in mice.

- 2210 • As a sanity check for model fit, we tested whether the frequency of
2211 stimulus- and history-congruent trials in the Confidence database²⁰ and
2212 IBL database²¹ correlate with the estimated parameters α and H , respec-
2213 tively. As expected, the estimated sensitivity toward stimulus information α
2214 was positively correlated with the frequency of stimulus-congruent percep-
2215 tual choices (humans: $\beta = 8.4 \pm 0.26$, $T(4.31 \times 10^3) = 32.87$, $p = 1.3 \times 10^{-211}$;
2216 mice: $\beta = 1.93 \pm 0.12$, $T(2.07 \times 10^3) = 16.21$, $p = 9.37 \times 10^{-56}$). Likewise, H was
2217 negatively correlated with the frequency of history-congruent perceptual
2218 choices (humans: $\beta = -11.84 \pm 0.5$, $T(4.29 \times 10^3) = -23.5$, $p = 5.16 \times 10^{-115}$;
2219 mice: $\beta = -6.18 \pm 0.66$, $T(2.08 \times 10^3) = -9.37$, $p = 1.85 \times 10^{-20}$).
- 2220 • Our behavioral analyses reveal that humans and mice show significant effects
2221 of perceptual history that impaired performance in randomized psychophys-
2222 ical experiments^{24,28,30,31,43} (Figure 2A and 3A). We therefore expected that
2223 humans and mice underestimated the true hazard rate \hat{H} of the experimen-
2224 tal environments (Confidence database²⁰: $\hat{H}_{Humans} = 0.5 \pm 1.58 \times 10^{-5}$); IBL
2225 database²¹: $\hat{H}_{Mice} = 0.49 \pm 6.47 \times 10^{-5}$). Indeed, when fitting the bimodal
2226 inference model to the trial-wise perceptual choices, we found that the es-
2227 timated (i.e., subjective) hazard rate H was lower than \hat{H} for both humans
2228 ($\beta = -6.87 \pm 0.94$, $T(61.87) = -7.33$, $p = 5.76 \times 10^{-10}$) and mice ($\beta = -2.91$
2229 ± 0.34 , $T(112.57) = -8.51$, $p = 8.65 \times 10^{-14}$).

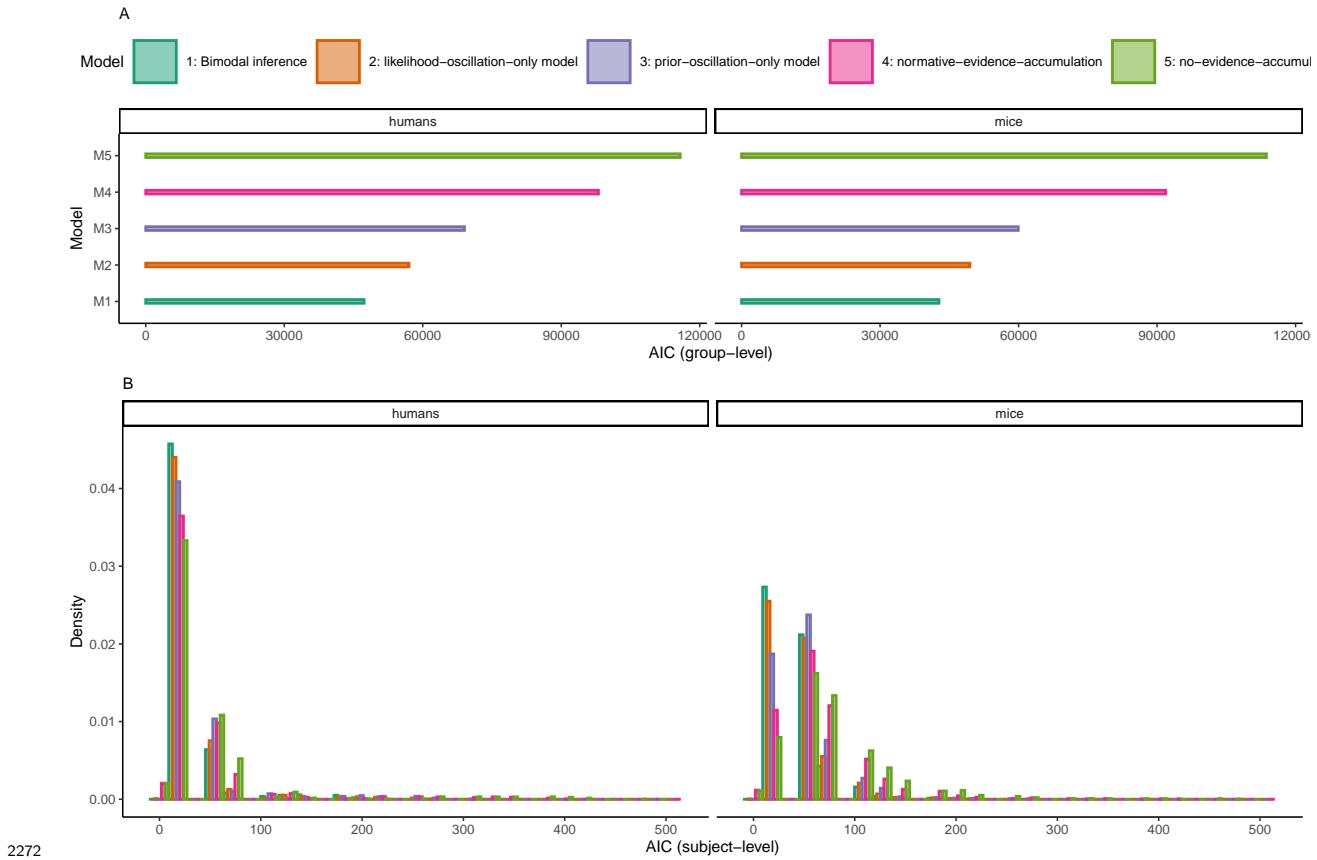
2230 • To further probe the validity of the bimodal inference model, we tested
2231 whether posterior model quantities could explain aspects of the behavioral
2232 data that the model was not fitted to. We predicted that the posterior
2233 decision variable L_t not only encodes perceptual choices (i.e., the variable
2234 used for model estimation), but should also predict the speed of response
2235 and subjective confidence^{30,44}. Indeed, the estimated trial-wise posterior
2236 decision certainty $|L_t|$ correlated negatively with RTs in humans ($\beta = -4.36 \times$
2237 $10^{-3} \pm 4.64 \times 10^{-4}$, $T(1.98 \times 10^6) = -9.41$, $p = 5.19 \times 10^{-21}$) and TDs mice
2238 ($\beta = -35.45 \pm 0.86$, $T(1.28 \times 10^6) = -41.13$, $p = 0$). Likewise, subjective
2239 confidence reports were positively correlated with the estimated posterior
2240 decision certainty in humans ($\beta = 7.63 \times 10^{-3} \pm 8.32 \times 10^{-4}$, $T(2.06 \times 10^6) =$
2241 9.18 , $p = 4.48 \times 10^{-20}$).

2242 • The dynamic accumulation of information inherent to our model entails that
2243 biases toward perceptual history are stronger when the posterior decision
2244 certainty at the preceding trial is high^{30,31,51}. Due to the link between pos-
2245 terior decision certainty and confidence, we reasoned that confident percep-
2246 tual choices should be more likely to induce history-congruent perception at
2247 the subsequent trial^{30,31}. Indeed, logistic regression indicated that history-
2248 congruence was predicted by the posterior decision certainty $|L_{t-1}|$ (humans:
2249 $\beta = 8.22 \times 10^{-3} \pm 1.94 \times 10^{-3}$, $z = 4.25$, $p = 2.17 \times 10^{-5}$; mice: $\beta = -3.72 \times 10^{-3}$
2250 $\pm 1.83 \times 10^{-3}$, $z = -2.03$, $p = 0.04$) and subjective confidence (humans: $\beta =$
2251 $0.04 \pm 1.62 \times 10^{-3}$, $z = 27.21$, $p = 4.56 \times 10^{-163}$) at the preceding trial.

2252 • As a third validation of the bimodal inference model, we used the posterior
2253 model parameters to simulate synthetic perceptual choices and repeated the
2254 behavioral analyses conducted for the empirical data. Simulations from the
2255 bimodal inference model closely replicated our empirical results: Simulated

perceptual decisions resulted from a competition of perceptual history with incoming sensory signals (Figure 4A). Stimulus- 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^{28,30,44} (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.



- 2273 • **Supplemental Figure S9. Comparison of the bimodal inference model against**
- 2274 **reduced control models.**
- 2275 • **A. Group-level AIC.** The bimodal inference model (M1) achieved the lowest
- 2276 AIC across the full model space ($AIC_1 = 4.73 \times 10^4$ in humans and 4.28×10^4
- 2277 in mice). Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and
- 2278 Model M3 ($AIC_3 = 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated
- 2279 only oscillations of either likelihood or prior precision. Model M4 ($AIC_4 =$
- 2280 9.8×10^4 in humans and 9.19×10^4 in mice) lacked any oscillations of likelihood
- 2281 and prior precision and corresponded to the normative model proposed by
- 2282 Glaze et al.⁵¹. In model M5 ($AIC_5 = 1.16 \times 10^5$ in humans and 1.14×10^5 in
- 2283 mice), we furthermore removed the integration of information across trials,
- 2284 such that perception depended only in incoming sensory information.

2285 • **B. Subject-level AIC.** Here, we show the distribution of AIC values at the
2286 subject-level. AIC for the bimodal inference model tended to be smaller
2287 than AIC for the comparator models (statistical comparison to the second-
2288 best model M2 in humans: $\beta = -1.81 \pm 0.27$, $T(5.07 \times 10^3) = -6.82$, $p =$
2289 1.02×10^{-11} ; mice: $T(1.5 \times 10^3) = -6.28$, $p = 4.38 \times 10^{-10}$).

2290 In the light of our response to Comments 1 - 9 above, we agree that a complete and ex-
2291 tensive investigation of the relation between bimodal inference, learning about changes in
2292 the environment and the relation to metacognition may be beyond the scope of the cur-
2293 rent manuscript: Both Reviewer 1 and 3 (see below) have shared that the manuscript is
2294 too long and should be streamlined. Yet evaluating the full model space (e.g., comparing
2295 update rules for inferences about H and M , testing for an influence of beliefs about M on
2296 learning about H etc.) would make the manuscript even longer. We are therefore happy to
2297 follow Prof. Fristons suggestions to omit section 5.8. We have changed the manuscript in
2298 the following ways:

2299 When introducing ω_{LLR} , we identify it as the precision afforded to the likelihood, referring
2300 to the Bayesian framework, and refer to fluctuations in mode as a hyperprior.

2301 • To allow for *bimodal inference*, i.e., alternating periods of internally- and
2302 externally-biased modes of perceptual processing that occur irrespective of
2303 the sequence of preceding experiences, we assumed that likelihood and prior
2304 vary in their influence on the perceptual decision according to fluctuations
2305 governed by ω_{LLR} and ω_ψ . These anti-phase sine functions (defined by am-
2306 plitudes $a_{LLR/\psi}$, frequency f and phase p) determine the precision afforded
2307 to the likelihood and prior⁵³. The implicit anti-phase fluctuations are man-
2308 dated by Bayes-optimal formulations in which inference depends only on the
2309 relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴).
2310 As such, ω_{LLR} and ω_ψ implement a hyperprior⁵⁵ in which the likelihood

2311 and prior precisions are shifted against each other at a dominant timescale
2312 defined by f

2313 We have deleted the section 5.8 and added a summary of our modeling approach to the
2314 discussion, closely following the text recommended by Prof. Friston:

2315 • (...) Yet relying too strongly on serial dependencies may come at a cost: When
2316 accumulating over time, internal predictions may eventually override exter-
2317 nal information, leading to circular and false inferences about the state of
2318 the environment⁵⁷. Akin to the wake-sleep-algorithm in machine learning⁵⁸,
2319 bimodal inference may help to determine whether errors result from ex-
2320 ternal input or from internally-stored predictions: During internal mode,
2321 sensory processing is more strongly constrained by predictive processes that
2322 auto-encode the agent's environment. Conversely, during external mode,
2323 the network is driven predominantly by sensory inputs¹⁸. Between-mode
2324 fluctuations may thus generate an unambiguous error signal that aligns in-
2325 ternal predictions with the current state of the environment in iterative
2326 test-update-cycles⁵⁸. On a broader scale, between-mode fluctuations may
2327 thus regulate the balance between feedforward versus feedback contribu-
2328 tions to perception and thereby play a adaptive role in metacognition and
2329 reality monitoring⁵⁹.

2330 • From the perspective of the Bayesian brain hypothesis, we hypothesized
2331 that observers have certain hyperpriors that are apt for accommodating
2332 fluctuations in the predictability of their environment, i.e., people believe
2333 that their world is inherently volatile. To be Bayes optimal, it is therefore
2334 necessary to periodically re-evaluate posterior beliefs about the parameters
2335 that define an internal generative model of the external sensory environment.

2336 One way to do this is to periodically suspend the precision of prior beliefs and
2337 increase the precision afforded to sensory evidence, thus updating Bayesian
2338 beliefs about model parameters.

- 2339 • The empirical evidence above suggests that the timescale of this periodic
2340 scheduling of evidence accumulation may be scale-invariant. This means
2341 that there may exist a timescale of periodic fluctuations in precision over
2342 every window or length of perceptual decision-making. Bimodal inference
2343 predicts perceptual decisions under a generative model (based upon a haz-
2344 ard function to model serial dependencies between subsequent trials) with
2345 periodic fluctuations in the precision of sensory evidence relative to prior
2346 beliefs at a particular timescale. Remarkably, a systematic model compari-
2347 son based on AIC indicated that a model with fluctuating precisions has
2348 much greater evidence, relative to a model in the absence of fluctuating pre-
2349 cisions. This ad-hoc addition of oscillations to a normative Bayesian model
2350 of evidence accumulation⁵¹ allowed us to quantify the dominant timescale
2351 of periodic fluctuations mode at approximately $0.11 \sqrt{1/N_{trials}}$ in humans and
2352 mice that is appropriate for these kinds of paradigms.

2353 Following our deletion of the section 5.8, we have adapted the last sentence of the abstract
2354 and the last paragraph of the introduction:

- 2355 • (...) We propose that between-mode fluctuations generate unambiguous error
2356 signals that enable optimal inference in volatile environments.
- 2357 • When less sensitive to external stimulus information, humans and mice did
2358 not behave more randomly, but showed stronger serial dependencies in their
2359 perceptual choices^{22–33}. These serial dependencies may be understood as driven by
2360 internal predictions that reflect the autocorrelation of natural environments³⁴ and bias

2361 perception toward preceding experiences^{30,31,35}. Computational modeling indicated that
2362 ongoing changes in perceptual performance may be driven by systematic fluctuations be-
2363 tween externally- and internally-oriented modes of sensory analysis. **We suggest that**
2364 **such *bimodal inference* may help to build stable internal representations of**
2365 **the sensory environment despite an ongoing stream of sensory information..**

2366 **10.1.10 Comment 11**

2367 This begs the question as to whether you want to pursue the 1/f story. You
2368 refer to this as “noise”. However, there is no noise in this setup. I think what
2369 you meant was that the fluctuations are scale free, because they evinced a power
2370 law. I am sure that there are scale free aspects of these kinds of hyperpriors;
2371 however, in the context of your paradigm I wonder whether you should just
2372 ignore the scale free aspect and focus on your estimated temporal scale implicit
2373 in f . This means you don’t have to hand wave about self-organized criticality in
2374 the discussion and focus upon your hypothesis.

2375 We would like to thank the reviewer for this suggestion. We agree that the discussion of self-
2376 organized criticality is far from the data. We have omitted this section from the discussion.
2377 With respect to f , we have adapted the manuscript to make clear that it captures the
2378 dominant timescale of fluctuations in mode:

- 2379 • (...) This implements a hyperprior⁵⁵ in which the likelihood and prior pre-
2380 cisions are shifted against each other at a dominant timescale defined by f :
2381 (...)
- 2382 • (...) The parameter f captured the dominant time scale at which likelihood
2383 and prior precision were shifted against each other and was estimated at
2384 0.11 $1/N_{trials}$ in both humans and mice.

2385 • Remarkably, a systematic model comparison based on AIC indicated that
2386 a model with fluctuating precisions has much greater evidence, relative to
2387 a model in the absence of fluctuating precisions. The ad-hoc addition of
2388 oscillations to a normative Bayesian model of evidence accumulation⁵¹ al-
2389 lowed us to quantify the dominant timescale of periodic fluctuations mode
2390 at approximately $0.11 \sqrt{N_{trials}}$ in humans and mice that is appropriate for
2391 these kinds of paradigms.

2392 **10.1.11 Comment 12**

2393 A final move—to make the paper more focused and digestible—would be to
2394 put a lot of your defensive analyses (e.g. about general arousal et cetera) in
2395 supplementary material. You have to be careful not to exhaust the reader by
2396 putting up a lot of auxiliary material before the important messages in your
2397 report.

2398 We have followed this suggestion and move the following sections to the supplement: section
2399 5.3 (Internal and external modes of processing facilitate response behavior and enhance
2400 confidence in human perceptual decision-making), section 5.4 (Fluctuations between internal
2401 and external mode modulate perceptual performance beyond the effect of general response
2402 biases), section 5.5 (Internal mode is characterized by lower thresholds as well as by history-
2403 dependent changes in biases and lapses). We have also moved secondary statistics to the
2404 figure legends and to the legends.

2405 **Minor points**

2406 **10.1.12 Comment 13**

2407 I cannot resist suggesting that you change your title to “Bimodal Inference in
2408 Mice and Men”

2409 We thank you for this suggestion and have changed the title accordingly.

²⁴¹⁰ 10.1.13 Comment 14

²⁴¹¹ Please replace “infra-slow fluctuations” with “slow fluctuations”. Slow has some
²⁴¹² colloquial meaning in fMRI studies but not in any scale free context.

²⁴¹³ Done.

²⁴¹⁴ 10.1.14 Comment 15

²⁴¹⁵ Please replace “simulated data” with “simulations” in the abstract. Finally,
²⁴¹⁶ please replace “robust learning and metacognition in volatile environments” with
²⁴¹⁷ “enable optimal inference and learning in volatile environments.”

²⁴¹⁸ Done. Since we have followed the suggestion to delete section 5.8, we have rephrased the
²⁴¹⁹ last paragraph of the abstract into (...) We propose that between-mode fluctuations
²⁴²⁰ generate unambiguous error signals that enable optimal inference in volatile
²⁴²¹ environments.

²⁴²² 10.1.15 Comment 16

²⁴²³ Line 50, please replace “about the degree of noise inherent in encoding of sen-
²⁴²⁴ sory information” with “the precision of sensory information relative to prior
²⁴²⁵ (Bayesian) beliefs.”

²⁴²⁶ Done.

²⁴²⁷ 10.1.16 Comment 17

²⁴²⁸ Line 125: please replace “a source of error” with “a source of bias”

²⁴²⁹ Done.

2430 10.1.17 Comment 18

2431 Line 141: please replace “one 1/f noise” with a scale-invariant process with a
2432 1/f power law” (here and throughout) this is not “noise” it is a particular kind
2433 of fluctuation.

2434 Done.

2435 10.1.18 Comment 19

2436 Line 178, when you say that the fluctuations may arise due to “changes in level
2437 of tonic arousal or on-task attention”, I think you need to qualify this. In
2438 predictive processing, on-task attention is exactly the modulation of sensory
2439 precision, relative to prior precision that you are characterizing here. Tonic
2440 arousal may be another thing may or may not confound your current results.

2441 Thank you very much for pointing this out. We have adapted the discussion to make the
2442 distinction between attention in the predictive processing sense and the broader issue of
2443 task engagement (reflecting fluctuations in arousal, fatigue etc.) clearer (see also comments
2444 above):

2445 • As a functional explanation for bimodal inference, we propose that percep-
2446 tion temporarily disengages from internal predictions to form stable infer-
2447 ences about the statistical properties of the sensory environment. Between-
2448 mode fluctuations may thus elude circular inferences that occur when both
2449 the causes and the encoding of sensory stimuli are volatile^{19,57}). By the
2450 same token, we suggest that fluctuations in mode occur at the level of perceptual
2451 processing^{26,30,46,47}, and are not a passive phenomenon that is primarily driven by fac-
2452 tors situated up- or downstream of sensory analysis.

2453 • How does attention relate between-mode fluctuations? According to pre-

2454 dictive processing, attention corresponds to the precision afforded to the
2455 probability distributions that underlie perceptual inference⁵³. As outlined
2456 above, between-mode fluctuations can be understood as ongoing shifts in the
2457 precision afforded to likelihood (*external mode*) and prior (*internal mode*),
2458 respectively. When the precision afforded to prior or likelihood increases,
2459 posterior precision increases, which leads to faster RTs and higher confi-
2460 dence. When defined from the perspective of predictive processing as the
2461 precision afforded to likelihood and prior⁵³, fluctuations in attention may
2462 thus provide a plausible explanation for the quadratic relationship between
2463 mode and RTs and confidence (Figure 2H and J; Figure 3I; Figure 3I).

- 2464 • Outside of the predictive processing field, attention is often understood in
2465 the context of task engagement⁶³, which varies according to the availability
2466 of cognitive resources that are modulated by factors such as tonic arousal, fa-
2467 miliarity with the task, or fatigue⁶³. Our results suggest that internal mode
2468 processing cannot be completely reduced to intervals of low task engage-
2469 ment: In addition to shorter RTs and elevated confidence, choices during
2470 internal mode were not random or globally biased, but driven by percep-
2471 tual history (Supplemental Figures S6-7). Moreover, our computational
2472 model identified the dominant timescale of between-mode fluctuations at
2473 0.11 1/ N_{trials} , which may be compatible with fluctuations in arousal⁶⁴, but
2474 is faster than to be expected for the development of task familiarity or fa-
2475 tigue.
- 2476 • However, in interpreting the impact of between-mode fluctuations on per-
2477 ceptual accuracy, speed of response and confidence, it is important to con-
2478 sider that global modulators such as tonic arousal are known to have non-
2479 linear effects on task performance⁶⁵: In perceptual tasks, performance seems

2480 so be highest during mid-level arousal, whereas low- and high-level arousal
2481 lead to reduced accuracy and slower responses⁶⁵. This contrasts with the
2482 effects of bimodal inference, where accuracy increases linearly as one moves
2483 from internal to external mode, and responses become faster at both ends
2484 of the mode spectrum.

- 2485 • Of note, high phasic arousal has been shown to suppress multi-domain bi-
2486 ases in decision-making in humans and mice^{66–68}, including the biases toward
2487 perceptual history²⁸ that we implicate in internal mode processing. The in-
2488 crease in response speed and history congruence over time (Supplemental
2489 Section 9.4) may argue against insufficient training as an alternative expla-
2490 nation for internal mode processing, but may also taken as a sign of waning
2491 arousal. The multiple mechanistic mappings to RTs and confidence there-
2492 fore warrant more direct measures of arousal (such as pupil size^{28,65,66,68–70},
2493 motor behavior^{69,70}, or neural data⁷¹) to better delineate bimodal inference
2494 from fluctuations in global modulators of task performance.

2495 **10.1.19 Comment 20**

2496 When introducing Equation 2, please make it clear that the omega terms stand in
2497 for the precisions afforded to the likelihood (`omega_llr`) and prior (`omega_`)
2498 that constitute the log posterior.

2499 We have modified the introduction of equation 2 as follows:

- 2500 • Following Bayes' theorem, we reasoned that binary perceptual decisions depend on the
2501 log posterior ratio L of the two alternative states of the environment that participants
2502 learn about via noisy sensory information⁵¹. We computed the posterior by combining
2503 the sensory evidence available at time-point t (i.e., the log likelihood ratio LLR) with

2504 the prior probability ψ , weighted by the respective precision terms ω_{LLR} and
 2505 ω_ψ :

$$L_t = LLR_t * \omega_{LLR} + \psi_t(L_{t-1}, H) * \omega_\psi \quad (25)$$

2506 You can then motivate Equation 6 and 7 as implementing the hyperprior in
 2507 which the sensory and prior precisions fluctuate at a particular time scale.

2508 We would like to thank the reviewer for this suggestion, which we have added to the intro-
 2509 duction of equations (6) and (7):

- 2510 • To allow for *bimodal inference*, i.e., alternating periods of internally- and
 2511 externally-biased modes of perceptual processing that occur irrespective of
 2512 the sequence of preceding experiences, we assumed that likelihood and prior
 2513 vary in their influence on the perceptual decision according to fluctuations
 2514 governed by ω_{LLR} and ω_ψ . These anti-phase sine functions (defined by am-
 2515 plitudes $a_{LLR/\psi}$, frequency f and phase p) determine the precision afforded
 2516 to the likelihood and prior⁵³. The implicit anti-phase fluctuations are man-
 2517 dated by Bayes-optimal formulations in which inference depends only on the
 2518 relative values of prior and likelihood precision (i.e., the Kalman gain⁵⁴).
 2519 As such, ω_{LLR} and ω_ψ implement a hyperprior⁵⁵ in which the likelihood
 2520 and prior precisions are shifted against each other at a dominant timescale
 2521 defined by f :

$$\omega_{LLR} = a_{LLR} * \sin(f * t + p) + 1 \quad (26)$$

$$\omega_\psi = a_\psi * \sin(f * t + p + \pi) + 1 \quad (27)$$

2522 10.1.20 Comment 21

2523 You can also point out that the implicit anti-phase fluctuations are mandated
2524 by Bayes optimal formulations in which it is only the relative values of the prior
2525 and sensory precision that matter. Bayesian filters these precisions constitute
2526 the Kalman gain. You can find a derivation of why this in treatments of the
2527 hierarchical Gaussian filter is by Mathys et al.

2528 We would like to thank the reviewer for this suggestion. We added this information to the
2529 description of our model in the Results section (see comment above).

2530 10.1.21 Comment 22

2531 In your first model simulations, I would make it clear in the main text which
2532 parameters you are optimizing's; namely (H, alpha, a_likelihood, a_prior f).
2533 Perhaps a little table with a brief description of the meaning of these hyper
2534 parameters would be useful?

2535 We now identify the optimized parameters at the outset of the modeling section:

- 2536 • (...) We used a maximum likelihood procedure to fit the bimodal infer-
2537 ence model (M1, Figure 1F) to the behavioral data from the Confidence
2538 database²⁰ and the IBL database²¹, optimizing the parameters α , H , amp_{LLR} ,
2539 amp_ψ , f and p (see Methods for details and Supplemental Table T2 for a sum-
2540 mary of the parameters of the bimodal inference model). We validated our
2541 model in three steps: (...).

2542 We furthermore included a table summarizing the model parameters in the Supplement:

2543 **10.1.22 Comment 23**

2544 Please remove Section 5.8. If you do not, you need to explain why — on line
2545 586 - setting $a = 0$ is appropriate when $a = 0$, the log posterior in Equation 2 is
2546 zero because the precisions (omegas) are zero (by Equations 6 and 7).

2547 We have removed the section 5.8. When setting the amplitude parameters to zero, ω_{LLR} and
2548 ω_ψ are constant at 1, creating a unimodal control model that corresponds to the normative
2549 Bayesian evidence accumulation model proposed by Glaze et al⁵¹.

2550 **10.2 Reviewer 2**

2551 The authors elucidate whether periodicities in the sensitivity to external infor-
2552 mation represent an epiphenomenon of limited processing capacity or, alterna-
2553 tively, result from a structured and adaptive mechanism of perceptual infer-
2554 ence. Analyzing large datasets of perceptual decision-making in humans and
2555 mice, they investigated whether the accuracy of visual perception is constant
2556 over time or whether it fluctuates. The authors found significant autocorrela-
2557 tions on the group level and on the level of individual participants, indicating
2558 that a stimulus-congruent response in a given trial increased the probability of
2559 stimulus-congruent responses in the future. Furthermore, the authors addressed
2560 whether observers cycle through periods of enhanced and reduced sensitivity to
2561 external information or whether observers rely on internal information in certain
2562 phases. This was quantified by whether a response at a given trial was correlated
2563 with responses in previous trials. The authors used computational modeling to
2564 infer the origin of the different modes (internal vs. external).

2565 **Evaluation**

2566 This is a very interesting and well-written manuscript, dealing with an important
2567 question. The findings are novel and provide an innovative account of interpret-

2568 ing visual perception. I am not an expert in modeling, so I will restrict my
2569 comments to theoretical framework and the experimental approach. I have a
2570 few minor questions that I would like the authors to answer or clarify.

2571 We would like to thank the reviewer for the evaluation of our manuscript. We have added
2572 the discussion of potential effects at the motor-level to our discussion.

2573 **Minor questions**

2574 **10.2.1 Comment 1**

2575 History congruent perception was defined on the basis of response repetitions.
2576 Are we really sure that responses are repeated due to some variant of a per-
2577 ceptual decision process (internal or external) or may arise on the motor-level -
2578 independent of a perceptual source? For instance, a response primed by residual
2579 activation in the motor system may represent a local effect independent from
2580 a general response bias. If indeed, a response repetition is initiated by what-
2581 ever reasons (non-perceptual), wouldn't this imply that the repeated response
2582 is per se more related to previous than to current visual information and would
2583 hence signal a reduced sensitivity to current external information? The authors
2584 are discussing the option of stereotypically repeated responses in the context
2585 of alertness. However, a tendency to repeat responses may arise due to other
2586 reasons. For instance, may the motor priming effects mentioned possibly explain
2587 faster RTs along with a stronger bias when in internal-mode.

2588 Thanks a lot for pointing this out. In this manuscript, we attempt to characterize the
2589 phenomenon of bimodal inference at the level of behavior: The Confidence database consists
2590 only of behavioral data. At the time of publishing this paper as a preprint, the IBL database
2591 had also released only behavioral data.

2592 We realize that is very difficult to preclude influences from effects that occur at the level of

2593 behavior. Not all studies in the confidence database have used a counter-balanced mapping
2594 between the perceptual decision and the associated motor-response. In the IBL data, the
2595 mapping between the perceptual decision and the associated motor-response is fixed (turning
2596 a response wheel left or right depending on the perceived location of a grating). Confidence
2597 reports also provide only indirect information on motor- vs. perceptual effects. One may
2598 speculate that, if a response was driven by residual activity in the motor system, it may
2599 be more likely to be a lapse and be accompanied by reduced confidence. We found that
2600 confidence was, on average, elevated for history-congruent choices.

2601 That being said, behavioral analyses alone are insufficient to rule out the contribution of
2602 motor-related effects to seriality in choices. This would require analyses of additional types
2603 of data, such as video tracking of the motor response or even neural data collected in brain
2604 areas directly related to motor behavior. While this analysis is beyond the scope of the
2605 present manuscript, we plan to carry out these analyses using the recent data publication of
2606 the IBL, that contains, among others, video tracking of the motor response (turning of the
2607 response wheel) and neuropixel recording across the whole brain, including premotor and
2608 motor cortex⁷¹.

2609 We have added these considerations to the discussion of potential confounds:

- 2610 • **Residual activation of the motor system may provide another contribu-**
2611 **tion to serial biases in perceptual choices⁷². Such motor-driven priming**
2612 **may lead to errors in randomized psychophysical designs, resembling the**
2613 **phenomenon that we identify as internally-biased processing⁷³. Moreover,**
2614 **residual activation of the motor system may lead to faster responses, and**
2615 **thus constitutes an alternative explanation for the quadratic relationship**
2616 **of mode with RTs⁷². The observation of elevated confidence for stronger**
2617 **biases toward internal mode speaks against the proposition that residual**
2618 **activation of the motor system is the primary driver of serial choice biases,**

2619 since strong motor-driven priming should lead to frequent lapses that are
2620 typically associated reduced confidence⁷⁴. Likewise, perceptual history ef-
2621 fects have repeatedly been replicated in experiments with counter-balanced
2622 stimulus-response mappings³⁰: Feigin2021.

- 2623 • No-response paradigms, in which perceptual decision are inferred from eye-
2624 movements alone, could help to better differentiate perceptual from motor-
2625 related effects. Likewise, video-tracking of response behavior and neural
2626 recording from motor- and premotor, which has recently been released for
2627 the IBL database⁷¹, may provide further insight into the relation of motor
2628 behavior to the perceptual phenomenon of between-mode fluctuations.

2629 10.3 Reviewer 3

2630 In this paper the authors propose that during perceptual decisions, humans and
2631 mice exhibit regular oscillatory fluctuations between an “external” (that places
2632 more weight on the perceptual evidence) and an “internal” (that places more
2633 weight on historical experiences) mode. In particular, the authors propose a
2634 computational scheme in which the influences of history and current stimulus
2635 on choice oscillate in anti phase, effectively implementing “bimodal inference”.
2636 The computational advantages of these scheme as well as its relation to the
2637 underlying neurophysiology are discussed.

2638 Overall, the authors make a very interesting proposal about what drives slow
2639 fluctuations in perceptual performance during randomized two-alternative choice
2640 tasks. This proposal relates changes in accuracy with changes in serial choice
2641 biases, which is a timely and synthesizing contribution. Furthermore, this pro-
2642 posal is backed by analyses over several human datasets and a large dataset in
2643 mice.

2644 Despite its strong empirical contribution, the paper seems limited by the fact
2645 that alternative computational hypotheses are not adequately considered (or at
2646 least considered in a systematic way). At the same time, and although the paper
2647 is well written, some parts are overly technical.

2648 We would like to thank the Reviewer for the very helpful comments on our manuscript.
2649 We fully agree that the previous version of our manuscript did not consider alternative
2650 computational hypotheses in a systematic and adequate way. As we outline in more detail
2651 in our point-by-point-responses below, we have addressed this issue by adding a formal model
2652 comparison of the bimodal inference model to reduced models, including a normative models
2653 of Bayesian evidence accumulation. We have added null-hypothesis-testing for enhanced
2654 history-congruence during internal mode. We have also moved a number of defensive analyses
2655 to the supplement.

2656 **Major comments:**

2657 10.3.1 Comment 1

2658 The authors collapse across various datasets in which different tasks were em-
2659 ployed. However, some details on the nature of these different tasks and a
2660 discussion on the rationale of collapsing behavioral metrics across them is miss-
2661 ing. The authors mention that all tasks involved binary perceptual decisions.
2662 In some parts of the manuscript the term “false alarms” is mentioned, indicat-
2663 ing a detection protocol. Other terms in the methods section (e.g., “set size”)
2664 might need further clarification. Importantly, it is not clear how reaction times
2665 were calculated in the various tasks and whether some experiments involved free
2666 response paradigms while others interrogation/ cued paradigms (in which case
2667 RTs can be defined as the latency between the response cue and the response).

2668 We would like to thank the Reviewer for this important point. Regarding the rationale

2669 for collapsing across the studies in the Confidence database: Having found strong evidence
2670 of apparent between-mode fluctuations in a study on intermittent bistable perception¹⁹, our
2671 goal was to test whether between-mode fluctuations were a general phenomenon in perceptual
2672 decision-making. We thus had a lenient threshold for including studies from the Confidence
2673 database, i.e., all that addressed the domain of perception in 2AFC tasks. This has the
2674 advantage of looking at perceptual 2AFC decisions in general and indicated that history
2675 effects and bimodal inference are present in a wide variety of tasks.

2676 At the same time, collapsing across diverse set of experiments means that the stimuli, the
2677 timing and the way that responses were collected differed between them. To account for this
2678 variability, we included individual experiments as random factors in linear mixed modeling.
2679 We also made sure that perceptual performance is comparable across studies (Supplemental
2680 Figure S1A-B). While our analysis of the IBL database was mainly motivated by investigat-
2681 ing bimodal inference across species, it also allowed us to replicate our results in a highly
2682 standardized task that was collected across many individual subjects²¹. We have added the
2683 rationale for collapsing across studies with its advantages and disadvantages to the *Open*
2684 *questions and limitations* subsection of the discussion:

- 2685 • Our results suggest bimodal inference as a pervasive aspect in perceptual
2686 decision-making in humans and mice. However, a number of limitations and
2687 open questions have to be considered: First, this work sought to understand
2688 whether fluctuations between internal and external mode, which we initially
2689 observed in an experiment on bistable perception in humans¹⁹, are general
2690 phenomenon that occurs across a diverse set of perceptual decision-making
2691 tasks. Our analysis of the Confidence database²⁰ therefore collapsed across
2692 all available experiments on binary perceptual decision-making. Individual
2693 experiments differed with respect to the stimuli, the manipulation of diffi-
2694 culty, the timing of trials, and the way responses were collected, but were

2695 highly comparable with respect to the central variables of stimulus- and
2696 history-congruence (Supplemental Figure S1A-B).

2697 • The variability across experiments, which we considered as random effects
2698 in all statistical analyses, enabled us to assess whether bimodal inference
2699 represents a general phenomenon in perceptual decision-making, but lim-
2700 ited the precision at which we were able to investigate the relation of mode
2701 to behavioral variables such as timing, task difficulty, RT or confidence.
2702 This issue is partially resolved by our analyses of the IBL database, which
2703 replicated our findings in an experiment that was highly standardized with
2704 respect to timing, task difficulty, and behavioral read-out²¹. It will be an
2705 important task for future research to validate our results on bimodal infer-
2706 ence in a standardized dataset of comparable volume in humans, which is,
2707 to our knowledge, not yet available.

2708 We apologize for the lack of clarity regarding the way we queried the Confidence database.
2709 To select a broad variety of experiments on 2AFC perceptual decision-making, we Confidence
2710 database for studies from the *perception* category (excluding studies from the categories *cog-*
2711 *nitive*, *motor*, *memory* and *mixed*) and selected studies with 2AFC responses. Our previous
2712 version of the manuscript had mentioned the variable names given to the difficulty variable
2713 in the individual experiments (i.e., the name of the column in the individual .txt files pro-
2714 vided for every experiment in Confidence database). The term *false alarm* turned up in the
2715 discussion of lapses of attention and arousal, which we have re-written in response to Com-
2716 ment 19 by Reviewer 1 and Comment 6 by Reviewer 3. We now provide more information
2717 on the experiments and variables selected in the Method section:

2718 • We downloaded the human data from the Confidence database²⁰ on
2719 10/21/2020, limiting our analyses to the category *perception*. Within this
2720 category, we selected studies in which participants made binary perceptual

decisions between two alternatives. We excluded two experiments in which the average perceptual accuracy fell below 50%. After excluding these experiments, our sample consisted of 21.05 million trials obtained from 4317 human participants and 66 individual experiments (Supplemental Table 1). Out of the 66 included experiments, 62 investigated visual, 1 auditory, 2 proprioceptive, and 1 multimodal perception. 59 experiments were based on discrimination and 6 on detection, with one investigating both.

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

10.3.2 Comment 2

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

2747 We would like to thank the reviewer for highlighting this important point. Following this
2748 suggestion, we have explicitly tested our main hypothesis ($H1$: periods of reduced stimulus-
2749 congruence are periods of enhanced reliance on history-congruence) against the following
2750 null hypotheses:

- 2751 • $H0_1$: Periods of reduced stimulus-congruence are periods of enhanced random choices
2752 • $H0_2$: Periods of reduced stimulus-congruence are periods of enhanced general bias

2753 We present three sets of statistical analyses to test $H1$ against $H0_{1/2}$:

2754 First, we used logistic regression to predict individual choices. Under $H1$, one would expect
2755 a significant effect of perceptual history in a logistic regression model that predicts individ-
2756 ual choices from the external stimulus, perceptual history and general response bias. At
2757 the model level, one would expect higher AIC in a model without perceptual history as a
2758 predictor of individual choices, indicating that perceptual history influences choices beyond
2759 noise ($H0_1$) and general response bias ($H0_2$).

2760 In both humans and mice, we found a significant effect of perceptual history on choices
2761 while controlling for bias. When eliminating perceptual history as a predictor of individual
2762 choices, we found higher AIC (providing model-level evidence against $H0_1$ and $H0_2$). We
2763 complemented this analysis by computing AIC in individual observers (Supplemental Figure
2764 S4), and again found higher AIC in models from which perceptual history was eliminated.
2765 We have added the following analyses have been added to the main manuscript.

2766 Humans:

- 2767 • **Subsection: Fluctuations between internal and external mode cannot be**
2768 **reduced to general response biases or random choices**
- 2769 • **The core assumption of bimodal inference - that ongoing changes in the sen-**
2770 **sitivity to external information are driven by internal predictions induced**

via perceptual history - needs to be contrasted against two alternative hypotheses: When making errors, observers may not engage with the task and respond stereotypically, i.e., exhibit stronger general biases toward one of the two potential outcomes, or simply choose randomly. Logistic regression confirmed that perceptual history made a significant contribution to perception ($\beta = 0.11 \pm 5.79 \times 10^{-3}$, $z = 18.53$, $p = 1.1 \times 10^{-76}$) over and above the ongoing stream of external sensory information ($\beta = 2.2 \pm 5.87 \times 10^{-3}$, $z = 375.11$, $p = 0$) and general response biases toward ($\beta = 15.19 \pm 0.08$, $z = 184.98$, $p = 0$). When eliminating perceptual history as a predictor of individual choices at individual trials, AIC increased by $\delta_{AIC} = 1.64 \times 10^3$ (see Supplemental Figure S4A-B for parameter- and model-level inference at the level of individual observers).

Mice:

- In line with humans, mice were biased toward perceptual history in 54.03% $\pm 0.17\%$ of trials ($T(163) = -7.52$, $p = 3.44 \times 10^{-12}$; Figure 4A and Supplemental Figure S1D). Perceptual history effects remained significant ($\beta = 0.51 \pm 4.49 \times 10^{-3}$, $z = 112.84$, $p = 0$) when controlling for external sensory information ($\beta = 2.96 \pm 4.58 \times 10^{-3}$, $z = 646.1$, $p = 0$) and general response biases toward one of the two potential outcomes ($\beta = -1.78 \pm 0.02$, $z = -80.64$, $p = 0$). When eliminating perceptual history as a predictor of individual choices, AIC increased by $\delta_{AIC} = 1.48 \times 10^4$, arguing against the notion that choice randomness and general response bias are the only determinants of perceptual performance (see Supplemental Figure S4C-D for parameter- and model-level inference within individual mice).

Second, we analyzed dynamic changes in history- and stimulus-congruence (i.e., smoothed

probabilities for stimulus-congruence, history-congruence and general response bias in sliding 10 trial time-windows). Under H1, one would expect a significant negative correlation between the dynamic probability of stimulus- and history-congruence. At the model level, one would expect higher AIC in a model without history-congruence as a predictor of stimulus-congruence, indicating that changes in the probability of history-congruence influence stimulus-congruence beyond noise ($H0_1$) and general response bias ($H0_2$).

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

Humans:

- Finally, we ensured that fluctuations in stimulus- and history-congruence are linked to each other, while controlling for fluctuations in the strength of general response biases. When perceptual choices were less biased toward external information, participants relied more strongly on internal information acquired from perceptual history (and vice versa, $\beta = -0.05 \pm 5.63 \times 10^{-4}$, $T(2.1 \times 10^6) = -84.21$, $p = 0$), controlling for fluctuations in the strength of general response biases ($\beta = -0.06 \pm 5.82 \times 10^{-4}$, $T(2.1 \times 10^6) = -103.51$, $p = 0$).

- **(...) Likewise, eliminating the dynamic fluctuations in history-congruence as a predictor of fluctuations in stimulus-congruence yielded an increase in AIC by $\Delta\{AIC\} +$

2822 7.06×10^3 . These results provided model-level evidence against the null hypotheses
2823 that fluctuations in stimulus-congruence are driven exclusively by choice randomness
2824 or general response bias (see Supplemental Section 9.2 for an in-depth assessment of
2825 general response bias).**

2826 Mice:

2827 • **As in humans, fluctuations in the strength of history-congruent biases had a signifi-
2828 cant effect on stimulus-congruence ($\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$,
2829 $p = 0$) beyond the effect of ongoing changes in general response biases ($\beta_2 = -0.03 \pm$
2830 6.94×10^{-4} , $T(1.34 \times 10^6) = -48.14$, $p = 0$). Eliminating the dynamic fluctuations
2831 in history-congruence as a predictor of fluctuations in stimulus-congruence resulted in
2832 an increase in AIC by $\Delta\text{AIC} + 2.8 \times 10^4$. This confirmed that, in both humans
2833 and mice, perceptual performance is modulated by systematic fluctuations between
2834 externally- and internally-oriented modes of sensory processing that exist beyond gen-
2835 eral response bias (see Supplemental Section 9.2 for an in-depth assessment of general
2836 response bias).**

2837 Third, we analyzed full and history-conditioned psychometric curves in external and inter-
2838 nal mode as well as across modes. Under our main hypothesis that periodic reductions
2839 in sensitivity to external information are driven by increases in the impact of perceptual
2840 history, one would expect (i) a history-dependent increase in biases and lapses (effects of
2841 perceptual history), and (ii), a history-independent increase in threshold (reduced sensitivity
2842 to external information). Conversely, if what we identified as internal mode processing was
2843 in fact driven by random choices, one would expect (i), a history-independent increase in
2844 lapse (choice randomness), (ii), no change in bias (no effect of perceptual history), and (iii),
2845 reduced thresholds (reduced sensitivity to external information). In both humans and mice,
2846 we observed the pattern predicted by H1. In response to the comments by Reviewer 1 and

2847 3, we have significantly streamlined the manuscript and moved our assessment of psycho-
2848 metric functions to the supplement. We now provide a summary of our results in the main
2849 manuscript to make our reasoning with respect to $H0_1$ and $H1$ more explicit:

2850 Humans:

- 2851 • To confirm that changes in the sensitivity to external information are indica-
2852 tive of internal mode processing, we estimated full and history-dependent
2853 psychometric curves during internal, external, and across modes. If, as we
2854 hypothesized, internal mode processing reflects an enhanced impact of per-
2855 ceptual history, one would expect a history-dependent increase in biases and
2856 lapses as well as a history-independent increase in threshold. Conversely, if
2857 internal mode processing were driven by random choices, one would expect
2858 a history-independent increase in biases and threshold, and no change in
2859 bias. In line with our prediction, we found that internal mode processing
2860 was associated with a history-dependent increase in bias and lapse as well
2861 as a history-independent increase in threshold (Supplemental Section 9.3.1
2862 and Supplemental Figure S6). This confirms that internal mode processing
2863 is indeed driven by an enhanced impact of perceptual history.

2864 Mice:

- 2865 • When fitting full and history-conditioned psychometric curves to the data
2866 from the IBL database, we observed that internal mode processing was as-
2867 sociated with a history-dependent increase in bias and lapse as well as a
2868 history-independent increase in threshold (Supplemental Section 9.3.2 and
2869 Supplemental Figure S7). This provided further evidence for the hypothesis
2870 that internal mode processing is driven by an enhanced impact of perceptual
2871 history, as opposed to increased choice randomness.

2872 10.3.3 Comment 3

2873 From a mechanistic (sequential sampling) perspective, several previous papers
2874 have examined whether choice history biases influence the starting point or the
2875 drift rate of the evidence accumulation process. Under the former formulation,
2876 reliance on the evidence vs. reliance on the previous choice will be naturally
2877 anti-correlated (the less weight you place on the evidence the more impactful the
2878 choice history will be, assuming that the last choice is represented as a starting
2879 point bias). This seems to be mapping onto the computational model the authors
2880 describe, in which there is a weight on the prior, a weight on the likelihood and
2881 the assumption that these weights fluctuate in anti-phase. It is not obvious that
2882 this anti-phase relationship needs to be imposed ad-hoc. Or whether it would
2883 emerge naturally (using a mechanistic or Bayesian framework). More generally,
2884 the authors assert that without an external mechanism prior biases would be
2885 impossible to overcome, and this would misfit the data. However, it would be
2886 important to a) actually show that the results cannot be explained by a single
2887 mechanism in which the anti-phase relationship is emergent rather than ad-hoc,
2888 b) relate the current framework with previous mechanistic considerations of
2889 serial choice biases.

2890 We would like to thank the reviewer for pointing this out. We agree that both normative
2891 Bayesian and mechanistic drift diffusion are bound to lead to anti-correlated effects of sen-
2892 sory information and perceptual history *at the level of individual trials*. This, however, does
2893 not necessarily entail slow fluctuations in the impact of sensory information and perceptual
2894 history that evolve *over many consecutive trials*. We now provide a systematic model com-
2895 parison and discuss our model in relation to drift diffusion models and descriptive models
2896 that assume slow changes in the latent parameters underlying perceptual decision-making
2897 (such as Roy et al., Neuron 2021 or Ashwood et al. Nature Neuroscience et al. 2022). We

2898 also discuss the ad-hoc nature of the bimodal inference model in the subsection *Limitations*
2899 and open questions.

2900 • We used a maximum likelihood procedure to fit the bimodal inference model
2901 (M1, Figure 1F) to the behavioral data from the Confidence database²⁰ and
2902 the IBL database²¹, optimizing the parameters α , H , amp_{LLR} , amp_ψ , f and
2903 p (see Methods for details and Supplemental Table T2 for a summary of
2904 the parameters of the bimodal inference model). We validated our model
2905 in three steps: First, to show that bimodal inference does not emerge spont-
2906aneously in normative Bayesian models of evidence accumulation, but re-
2907quires the ad-hoc addition of anti-phase oscillations in prior and likelihood
2908 precision, we compared the bimodal inference model to four control models
2909 (M2-5, Figure 1G). In these models, we successively removed the anti-phase
2910 oscillations (M2-M4) and the integration of information across trials (M5)
2911 from the bimodal inference model and performed a model comparison based
2912 on AIC.

2913 • Model M2 ($AIC_2 = 5.7 \times 10^4$ in humans and 4.94×10^4 in mice) and Model
2914 M3 ($AIC_3 = 6.9 \times 10^4$ in humans and 5.99×10^4 in mice) incorporated only
2915 oscillations of either likelihood or prior precision. Model M4 ($AIC_4 = 9.8 \times 10^4$
2916 in humans and 9.19×10^4 in mice) lacked any oscillations of likelihood and
2917 prior precision and corresponded to the normative model proposed by Glaze
2918 et al.⁵¹. In model M5 ($AIC_4 = 1.16 \times 10^5$ in humans and 1.14×10^5 in mice), we
2919 furthermore removed the integration of information across trials, such that
2920 perception depended only in incoming sensory information (Figure 1G).

2921 • The bimodal inference model achieved the lowest AIC across the full model
2922 space ($AIC_1 = 4.73 \times 10^4$ in humans and 4.28×10^4 in mice) and was clearly
2923 superior to the normative Bayesian model of evidence accumulation (δ_{AIC}

2924 $= -5.08 \times 10^4$ in humans and -4.91×10^4 in mice; Supplemental Figure S9).

- 2925 • In sum, computational modeling suggested that between-mode fluctuations
2926 are best explained by two interlinked processes (Figure 1E): (i), the dynamic
2927 accumulation of information across successive trials mandated by normative
2928 Bayesian models of evidence accumulation and, (ii), ongoing anti-phase os-
2929 cillations in the impact of external and internal information.
- 2930 • Could bimodal inference emerge spontaneously in normative models of per-
2931 ceptual decision-making? In predictive processing, the relative precision of
2932 prior and likelihood determines their integration into the posterior that de-
2933 termines the content of perception. At the level of individual trials, the
2934 perceptual impact of internal predictions generated from perceptual history
2935 (prior precision) and external sensory information (likelihood precision) are
2936 thus necessarily anti-correlated. The same holds for mechanistic models of
2937 drift diffusion, which understand choice history biases as driven by changes
2938 in the starting point⁵¹ or the drift rate of evidence accumulation³². Under
2939 the former formulation, perceptual history is bound to have a stronger influ-
2940 ence on perception when less weight is given to incoming sensory evidence,
2941 assuming that the last choice is represented as a starting point bias. The
2942 effects of choice history in normative Bayesian and mechanistic drift diffu-
2943 sion models can be mapped onto one another via the Bayesian formulation
2944 of drift diffusion⁶⁰, where the inverse of likelihood precision determines the
2945 amount of noise in the accumulation of new evidence, and prior precision
2946 determines the absolute shift in its starting point⁶⁰.
- 2947 • While it is thus clear that the impact of perceptual history and sensory
2948 evidence are anti-correlated *at each individual trial*, we here introduce anti-
2949 phase oscillations as an ad-hoc modification to model slow fluctuations in

2950 prior and likelihood precision that evolve *over many consecutive trials* and
2951 are not mandated by normative Bayesian or mechanistic drift diffusion mod-
2952 els. The bimodal inference model provides a reasonable explanation of the
2953 linked autocorrelations in stimulus- and history-congruence, as evidenced
2954 by formal model comparison, successful prediction of RTs and confidence
2955 as out-of-training variables, and a qualitative reproduction of our empirical
2956 data from posterior model parameter as evidence against over- or under-
2957 fitting.

- 2958 • Of note, similar non-stationarities have been observed in descriptive mod-
2959 els that assume continuous⁶¹ or discrete¹² changes in the latent states that
2960 modulate perceptual decision-making at slow timescales. A recent compu-
2961 tational study⁶² has used a Hidden Markov model to investigate perceptual
2962 decision-making in the IBL database²¹. In analogy to our findings, the au-
2963 thors observed that mice switch between temporally extended *strategies*
2964 that last for more than 100 trials: During *engaged* states, perception was
2965 highly sensitive to external sensory information. During *disengaged* states,
2966 in turn, choice behavior was prone to errors due to enhanced biases toward
2967 one of the two perceptual outcomes⁶². Despite the conceptual differences to
2968 our approach (discrete states in a Hidden Markov model that correspond to
2969 switches between distinct decision-making strategies⁶² vs. gradual changes
2970 in mode that emerge from sequential Bayesian inference and ongoing fluc-
2971 tuations in the impact of external relative to internal information), it is
2972 tempting to speculate that engaged/disengaged states and between-mode
2973 fluctuations might tap into the same underlying phenomenon.
- 2974 • A third open question concerns the computational underpinnings of bimodal
2975 inference. The addition of slow anti-phase oscillations to the integration

2976 of prior and likelihood represents an ad-hoc modification of a normative
2977 Bayesian model of evidence accumulation⁵¹. While the bimodal inference
2978 model is supported by formal model comparison, the successful prediction
2979 of out-of-training variables and the qualitative reproduction of our empi-
2980 rical data in simulations from posterior model parameters, it is an impor-
2981 tant task for future research to test whether between-mode fluctuations can
2982 emerge spontaneously in hierarchical models of Bayesian inference, whether
2983 modes are continuous¹⁹ or discrete⁶², and whether bimodal inference can be
2984 causally manipulated by experimental variables. We speculate that between-
2985 mode fluctuations may separate the perceptual contribution of internal pre-
2986 dictions and external sensory data in time, creating unambiguous learning
2987 signals that benefit inference about the precision of prior and likelihood,
2988 respectively. This proposition should be tested empirically by relating the
2989 phenomenon of bimodal inference to performance in, e.g., reversal learning,
2990 probabilistic reasoning, or metacognition.

2991 10.3.4 Comment 4

2992 The authors need to unpack their definition of history biases since in previous
2993 work biases due to the response or the identity of the stimulus at the previous
2994 trial are treated differently. Here, the authors focus on response biases but it
2995 is not clear whether they could examine also stimulus-driven history biases (in
2996 paradigms where stimulus-response is remapped on each trial).

2997 We would like to thank the reviewer for raising this important point. We defined the history-
2998 biases reported in our main manuscript by comparing the *response about the perceived stimu-*
2999 *lus category (A vs. B) at the current and at the preceding trial (choice history)*. An alterna-
3000 *tive would have been to define history biases by comparing the choice at the current trial to*
3001 *the stimulus category presented at the preceding trial (stimulus history)*. As we show below,

3002 perceptual responses tended to be biased not only toward choice history, but also (but to a
3003 lesser degree) to stimulus history. This is expected, as perception was *stimulus-congruent* on
3004 approximately 75% of trials, causing the effects of the preceding response and the preceding
3005 stimulus to be highly correlated. We therefore compared the effects on choice history and
3006 stimulus history induced by trials at which perception was *stimulus-incongruent*, since those
3007 trials lead to opposite predictions regarding the perceptual choice at the subsequent trial.

3008 As expected, perceptual choices were attracted toward perceptual choices at preceding
3009 stimulus-incongruent trials (i.e., a positive effect of choice history). By contrast, percep-
3010 tual choices tended to be repelled away from the stimulus presented the preceding trial.
3011 This repulsion of choices away from stimuli presented at stimulus-incongruent trials con-
3012 firms that the choices at stimulus-incongruent trials were the primary driver of serial effects
3013 in perception in both humans and mice.

3014 We now refer to our analysis on stimulus history as an additional confound, which we present
3015 in detail in the Supplement 9.1 of our manuscript:

- 3016 • (...) These serial biases were effects of choice history, i.e., driven by the
3017 experiences reported at the preceding trial, and could not be attributed to
3018 stimulus history, i.e., to effects of the stimuli presented at the preceding trial
3019 (Supplemental Section 9.1).

3020 Supplement:

- 3021 • The main manuscript reports the effects of perceptual history, which we
3022 defined as the impact of the choice at the preceding trial on the choice at
3023 the current trial (henceforth *choice history*). *Stimulus history*, which is
3024 defined as the impact of the stimulus presented at the preceding trial on the
3025 choice at the present trial, represents an alternative approach to this. Here,
3026 we compare the effects of choice history to the effects of stimulus history.

- 3027 • We observed a significant bias toward stimulus history (humans: $49.76\% \pm$
3028 0.1% of trials, $\beta = 1.26 \pm 0.94$, $T(373.62) = 1.34$, $p = 0.18$; mice: $51.11\% \pm$
3029 0.08% of trials, $T(164) = 13.4$, $p = 3.86 \times 10^{-28}$). The bias toward stimulus
3030 history was smaller than the bias toward choice history (humans: $\beta = -3.53$
3031 ± 0.5 , $T(66.53) = -7.01$, $p = 1.48 \times 10^{-9}$; mice: $T(164) = -17.21$, $p = 1.43 \times$
3032 10^{-38}).
- 3033 • The attraction of choices toward both preceding choices and stimuli is ex-
3034 pected, as perception was *stimulus-congruent* on approximately 75% of
3035 trials, causing choices and stimuli to be highly correlated. We therefore
3036 compared the effects of choice history and stimulus history after *stimulus-*
3037 *incongruent* (i.e., *error*) trials, since those trials lead to opposite predictions
3038 regarding the perceptual choice at the subsequent trial.
- 3039 • As expected from the findings presented in the main manuscript, perceptual
3040 choices were attracted toward perceptual choices when the inducing trial was
3041 stimulus-incongruent (i.e., a positive effect of choice history; humans: $\beta =$
3042 $0.19 \pm 1.4 \times 10^{-4}$, $z = 1.36 \times 10^3$, $p = 0$; mice: $\beta = 0.92 \pm 0.01$, $z = 88.82$, $p = 0$).
3043 By contrast, perceptual choices tended to be repelled away from the stimulus
3044 presented at preceding stimulus-incongruent trial (i.e., a negative effect of
3045 stimulus history; humans: $\beta = -0.19 \pm 0.01$, $z = -16.47$, $p = 5.99 \times 10^{-61}$:
3046 mice: $\beta = -0.92 \pm 0.01$, $z = -88.76$, $p = 0$). This repulsion of choices away
3047 from stimuli presented at stimulus-incongruent trials confirmed that choices
3048 (which are anti-correlated to stimuli at stimulus-incongruent trials) were the
3049 primary driver of attracting serial effects in perception.
- 3050 • In sum, the above results suggest that, in both humans and mice, serial
3051 dependencies were better explained by the effects of choice history as op-
3052 posed to the effects of stimulus history. This aligns with a result recently

3053 published for the IBL database, where mice were shown to follow an *action-*
3054 *kernel* as opposed to a *stimulus-kernel* model when integrating information
3055 across trials⁸¹.

3056 10.3.5 Comment 5

3057 Previous work, which the authors acknowledges in their Discussion (6.5), distin-
3058 guishes repetitive history biases from alternating biases. For instance, in Braun,
3059 Urai & Donner (2018, JoN) participants are split into repetitive or alternating.
3060 Shouldn't the authors define the history bias in a similar fashion? The authors
3061 point out that attracting and repelling biases operate simultaneously across dif-
3062 ferent timescales. However, this is not warranted given Braun et. al and other
3063 similar papers. It is not clear how this more nuanced definition of history bias
3064 would alter the conclusions.

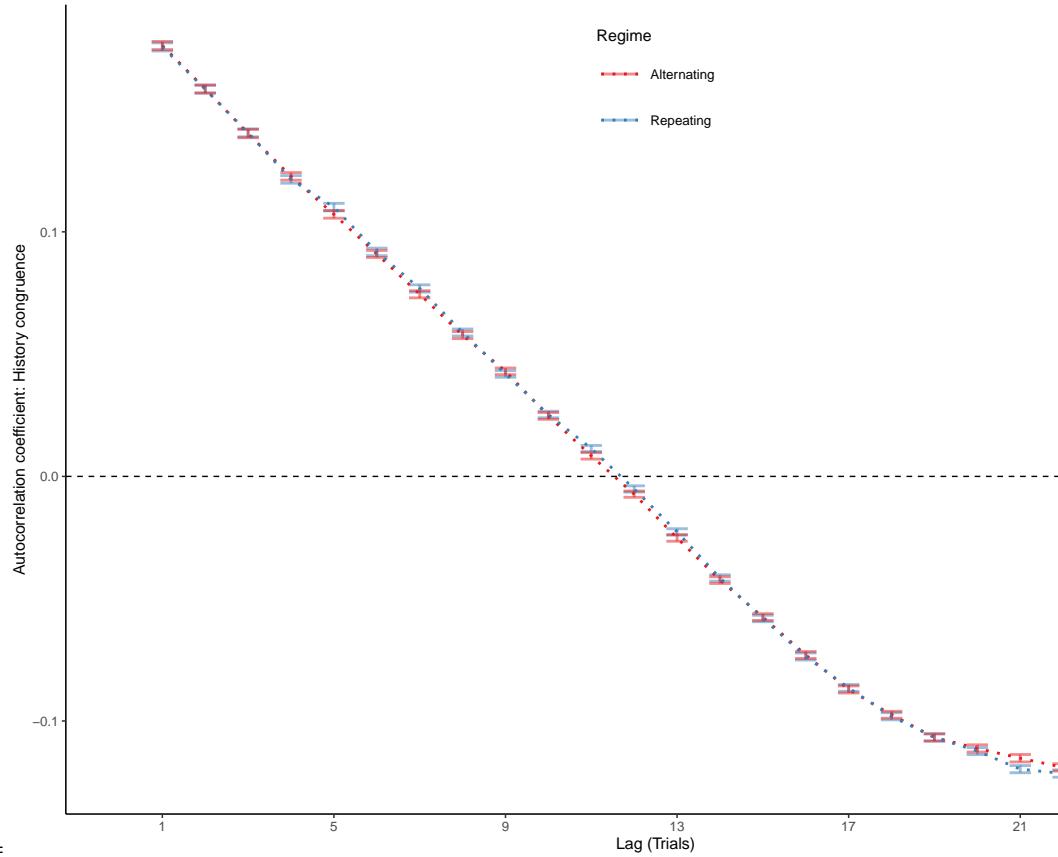
3065 We would like to thank the reviewer for raising this important point. Our empirical results
3066 show that, on average, history biases tend to be repetitive (Figure 2A, Figure 3A, and the
3067 biases in the psychometric functions in the Supplemental Figure S6-7). In fact, only 2 of the
3068 66 experiments we included from the Confidence database²⁰ showed significant alternating
3069 biases (Supplemental Figure S1, please note that history-congruence was not used in the
3070 inclusion algorithm). However, this does not rule out the possibility that there are periods
3071 of alternating biases in the other experiments with net repeating effects.

3072 Importantly, our central finding of autocorrelation in history-congruence does not distinguish
3073 between alternating and repetitive history biases. In the plot below, we show autocorrelation
3074 curves for fluctuations history-congruence for both alternation (hazard = 0.8) and repetition
3075 (hazard = 0.2). Both were simulated for 10 blocks of a random duration between 15 and 30
3076 trials, interleaved with 10 blocks with no history biases (hazard = 0.5). This simulation illus-
3077 trates that the autocorrelation of alternating and repeating biases is identical for symmetric
3078 pairs of hazard rates. The autocorrelation of history-congruence and the associated internal

3079 mode processing is therefore not tied to repeating biases, but accommodates alternating bi-
3080 ases as well (which seem to be, on average and in our data, less frequent). We therefore did
3081 not separate alternating from repeating biases in our analysis of mode.

3082 We apologize for not having recognized this aspect in the previous version of the discus-
3083 sion. We have rewritten the paragraph on alternating and repeating biases in the discussion,
3084 referring to the plot below, which we have added to the Supplemental Materials.

3085 • Second, our results point to an attraction of perception toward preceding
3086 choices. Previous work has shown that perceptual decision-making is con-
3087 currently affected by both attractive and repulsive serial biases that oper-
3088 ate on distinct time-scales and serve complementary functions for sensory
3089 processing^{27,75,76}: Short-term attraction may serve the decoding of noisy
3090 sensory inputs and increase the stability of perception, whereas long-term
3091 repulsion may enable efficient encoding and sensitivity to change²⁷. In the
3092 data analyzed here, history biases tended to be repetitive (Figure 2A, Figure
3093 3A, Supplemental Figure S6 and S7), as only 2 of the 66 experiments of the
3094 Confidence database²⁰ showed significant alternating biases (Supplemental
3095 Figure S1). However, as we show in Supplemental Figure S14, fluctuations
3096 in both alternating and repeating history biases generate overlapping auto-
3097 correlation curves. Our analysis of between-mode fluctuations is therefore
3098 not tied exclusively to repeating biases, but accommodates alternating biases
3099 as well, such that both may lead to internally-biased processing and reduced
3100 sensitivity to external sensory information. Future work could apply our ap-
3101 proach to paradigms that boost alternating as opposed to repeating biases,
3102 as this would help to better understand how repetition and alternation are
3103 linked in terms of their computational function and neural implementation²⁷.



3104 **Supplemental Figure S14**

- 3105 • Supplemental Figure S14. Autocorrelation of history-congruence of alternating
 3106 and repeating biases. Here, we simulate the autocorrelation of history-
 3107 congruence in 10^3 synthetic participants. In the repeating regime (blue),
 3108 history-congruence fluctuated between 50% and 80% (blue) in interleaved
 3109 blocks (10 blocks per condition with a random duration between 15 and
 3110 30 trials). In the alternation regime (red), history-congruence fluctuated
 3111 between 50% and 20%. The resulting autocorrelation curves for history-
 3112 congruence overlap, indicating that our analysis is able to accommodate
 3113 both repeating and alternating biases.

3114 **10.3.6 Comment 6**

3115 The arousal hypothesis seems to be ruled out too easily, merely in the presence
 3116 of a non-monotonic “state” vs. RT pattern. Arousal can have an inverted U-

3117 shaped effect on behavioral performance and recent paper has demonstrated
3118 a non-monotonic effect of tonic arousal (baseline pupil) on RTs and accuracy
3119 (<https://www.biorxiv.org/content/10.1101/2023.07.28.550956.abstract>). More
3120 generally, the RT and confidence analyses need to be complemented, perhaps by
3121 computational modeling using sequential sampling models, as these behavioral
3122 metrics have multiple mechanistic mappings (e.g., a fast RT might correspond
3123 to high SNR or an impulsive decisions driven by a starting point bias).

3124 We would like to thank the reviewer for this important point. Considering this Comment and
3125 the Comment 3 by Reviewer 1, we realize that the quadratic relationships between mode and
3126 RTs/confidence do not represent a convincing defensive analysis against the potential contri-
3127 butions of arousal to the phenomenon that we have identified as between-mode fluctuations.
3128 Rather, we now interpret the fluctuations of RTs/confidence with mode as indicative of a
3129 scenario in which between-mode fluctuations modulate a decision-variable that determines
3130 not only the perceptual choices, but also the speed and confidence at which they are made.

3131 Therefore, as a first response to this comment, we have re-phrased our assessment of RT and
3132 confidence in the following way:

3133 Humans:

- 3134 • The above results point to systematic fluctuations in the *decision variable*⁴⁴
3135 that determines perceptual choices, causing enhanced sensitivity to external
3136 stimulus information during external mode and increased biases toward pre-
3137 ceding choices during internal mode. As such, fluctuations in mode should
3138 influence downstream aspects of behavior and cognition that operate on the
3139 perceptual decision variable⁴⁴. To test this hypothesis with respect to mo-
3140 tor behavior and metacognition, we asked how bimodal inference relates to
3141 response times (RTs) and confidence reports. (...).

3142 • (...) In sum, the above results indicate that reporting behavior and metacog-
3143 nition do not map linearly onto the mode of sensory processing. Rather, they
3144 suggest that slow fluctuations in the respective impact of external and in-
3145 ternal information are most likely to affect perception at an early level of
3146 sensory analysis^{46,47}. Such low-level processing may thus integrate percep-
3147 tual history with external inputs into a decision variable⁴⁴ that influences
3148 not only perceptual choices, but also the speed and confidence at which they
3149 are made.

3150 • In what follows, we probe alternative explanations for between-mode fluc-
3151 tuations, test for the existence of modes in mice, and propose a predictive
3152 processing model that explains fluctuations in mode ongoing shifts in the
3153 precision afforded to external sensory information relative to internal pre-
3154 dictions driven by perceptual history.

3155 Mice:

3156 • The above results confirm that fluctuations between internally- and
3157 externally-biased modes generalize to perceptual decision-making in mice.
3158 As in humans, we hypothesized that bimodal inference modulates the
3159 decision variable⁴⁴ that determines not only perceptual choices, but also
3160 downstream aspects of mouse behavior⁴⁴. (...). When fitting full and
3161 history-conditioned psychometric curves to the data from the IBL database,
3162 we observed that internal mode processing was associated with a history-
3163 dependent increase in bias and lapse as well as a history-independent
3164 increase in threshold (Supplemental Section 9.3.2 and Supplemental Figure
3165 S7). Over time, the frequency of history-congruent choices increased
3166 alongside stimulus-congruence and speed of response as mice were exposed

3167 to the experiment, arguing against the proposition that biases toward
3168 perceptual history reflected an unspecific response strategy in mice who
3169 were not sufficiently trained on the IBL task.

3170 Second, we have re-structured the section of defensive analyses, where we contrast the phe-
3171 nomenon that we identify as fluctuating modes in perception with stereotypical or random
3172 responses as evidence of low task engagement, and not specifically with attention or arousal,
3173 which we discuss below. To streamline the manuscript, we report those analyses in detail in
3174 the Supplement (see Comments 12 by Reviewer 1 and Comment 9 by Reviewer 3).

3175 • The core assumption of bimodal inference - that ongoing changes in the sen-
3176 sitivity to external information are driven by internal predictions induced
3177 via perceptual history - needs to be contrasted against two alternative hy-
3178 potheses: When making errors, observers may not engage with the task and
3179 respond stereotypically, i.e., exhibit stronger general biases toward one of
3180 the two potential outcomes, or simply choose randomly. Logistic regression
3181 confirmed that perceptual history made a significant contribution to per-
3182 ception ($\beta = 0.11 \pm 5.79 \times 10^{-3}$, $z = 18.53$, $p = 1.1 \times 10^{-76}$) over and above
3183 the ongoing stream of external sensory information ($\beta = 2.2 \pm 5.87 \times 10^{-3}$, z
3184 = 375.11, $p = 0$) and general response biases toward ($\beta = 15.19 \pm 0.08$, $z =$
3185 184.98, $p = 0$).

3186 • When eliminating perceptual history as a predictor of individual choices
3187 at individual trials, AIC increased by $\delta_{AIC} = 1.64 \times 10^3$ (see Supplemental
3188 Figure S4A-B for parameter- and model-level inference at the level of indi-
3189 vidual observers). Likewise, when eliminating slow fluctuations in history-
3190 congruence as a predictor of slow fluctuations in stimulus-congruence across
3191 trials, we observed an increase in AIC by $\delta_{AIC} + 7.06 \times 10^3$. These results

3192 provided model-level evidence against the null hypotheses that fluctuations
3193 in stimulus-congruence are driven exclusively by choice randomness or gen-
3194 eral response bias (see Supplemental Section 9.2 for an in-depth assessment
3195 of general response bias).

- 3196 • To confirm that changes in the sensitivity to external information are indica-
3197 tive of internal mode processing, we estimated full and history-dependent
3198 psychometric curves during internal, external, and across modes. If, as we
3199 hypothesized, internal mode processing reflects an enhanced impact of per-
3200 ceptual history, one would expect a history-dependent increase in biases and
3201 lapses as well as a history-independent increase in threshold. Conversely, if
3202 internal mode processing were driven by random choices, one would expect
3203 a history-independent increase in biases and threshold, and no change in
3204 bias. In line with our prediction, we found that internal mode processing
3205 was associated with a history-dependent increase in bias and lapse as well as
3206 a history-independent increase in threshold (Supplemental Section 9.3 and
3207 Supplemental Figure S6-7). This confirmed that internal mode processing
3208 is indeed driven by an enhanced impact of perceptual history.
- 3209 • In line with this, the quadratic relationship between mode and confidence
3210 (Figure 2J) suggested that biases toward internal information do not reflect
3211 a post-perceptual strategy or repeating preceding choices when the subjec-
3212 tive confidence in the perceptual decision is low. Moreover, while responses
3213 became faster with increased exposure to the experiments of the Confi-
3214 dence database, the frequency of history-congruent choices increased over
3215 time, speaking against the proposition that participants may stereotypically
3216 repeat preceding choices when not yet familiar with the experimental task
3217 (see Supplemental Section).

- 3218 • Taken together, our results thus argue against recurring intervals of low task
3219 engagement, which may be signaled by stereotypical or random responses, as
3220 an alternative explanation for the phenomenon that we identify as bimodal
3221 inference.

3222 Third, in response the Comment 3 by Reviewer 1, we now interpret the quadratic relationship
3223 of mode to RTs/confidence in the context of predictive processing views on attention⁵³. Based
3224 on the Bayesian formulation of drift diffusion⁶⁰, we propose that the effects of likelihood on
3225 prior precision on the decision variable and, consequently, on confidence and RTs can be
3226 translated into the mechanistic framework of drift diffusion. Specifically, Bitzer et al. relate
3227 likelihood precision to noise in the accumulation process, and prior precision to the amount
3228 of shift in the starting point⁶⁰. As a third response to this comment, we have re-written
3229 our discussion of the quadratic relationship of mode to RTs and Confidence, focusing on
3230 predictive coding models attention, which we relate to mechanistic drift diffusion models:

- 3231 • How does attention relate between-mode fluctuations? According to pre-
3232 dictive processing, attention corresponds to the precision afforded to the
3233 probability distributions that underlie perceptual inference⁵³. As outlined
3234 above, between-mode fluctuations can be understood as ongoing shifts in the
3235 precision afforded to likelihood (*external mode*) and prior (*internal mode*),
3236 respectively. When the precision afforded to prior or likelihood increases,
3237 posterior precision increases, which leads to faster RTs and higher confi-
3238 dence. When defined from the perspective of predictive processing as the
3239 precision afforded to likelihood and prior⁵³, fluctuations in attention may
3240 thus provide a plausible explanation for the quadratic relationship of mode
3241 to RTs and confidence (Figure 2H and J; Figure 3I; Figure 4I). Such ef-
3242 ffects of attention in the predictive processing sense can be directly related
3243 to mechanistic drift diffusion models⁶⁰, where both larger shifts in starting

3244 point (related to increased prior precision in internal mode) and lower noise
3245 in the accumulation of evidence (related to increased likelihood precision in
3246 external mode) may explain faster and more confident responses.

3247 Given the correspondence between normative Bayesian and mechanistic drift diffusion model,
3248 we believe that we would not gain additional insights into the role of arousal and additional
3249 potential confounds or causes of between-mode fluctuations by fitting drift diffusion models
3250 as an alternative class of behavioral models to our data. To understand the relation of arousal
3251 to the bimodal inference, we think that it is necessary to look at data beyond behavior, such
3252 as pupillometry, video tracking of response behavior, or neural data. While this is beyond
3253 the scope of the current manuscript, we plan to do these analyses in a follow-up paper, using
3254 data published by the IBL after this paper was submitted. The IBL data now contains eye
3255 tracking, video tracking of response behavior, and neuropixel recordings across the whole
3256 mouse brain⁷¹. As a fourth response to this comment, we have re-written our discussion of
3257 attention and arousal:

- 3258 • Outside of the predictive processing field, attention is often understood in
3259 the context of task engagement⁶³, which varies according to the availability
3260 of cognitive resources that are modulated by factors such as tonic arousal, fa-
3261 miliarity with the task, or fatigue⁶³. Our results suggest that internal mode
3262 processing cannot be completely reduced to intervals of low task engage-
3263 ment: In addition to shorter RTs and elevated confidence, choices during
3264 internal mode were not random or globally biased, but driven by percep-
3265 tual history (Supplemental Figures S6-7). Moreover, our computational
3266 model identified the dominant timescale of between-mode fluctuations at
3267 0.11 1/ N_{trials} , which may be compatible with fluctuations in arousal⁶⁴, but
3268 is faster than to be expected for the development of task familiarity or fa-
3269 tigue.

- 3270 • However, in interpreting the impact of between-mode fluctuations on per-
3271 ceptual accuracy, speed of response and confidence, it is important to con-
3272 sider that global modulators such as tonic arousal are known to have non-
3273 linear effects on task performance⁶⁵: In perceptual tasks, performance seems
3274 so be highest during mid-level arousal, whereas low- and high-level arousal
3275 lead to reduced accuracy and slower responses⁶⁵. This contrasts with the
3276 effects of bimodal inference, where accuracy increases linearly as one moves
3277 from internal to external mode, and responses become faster at both ends
3278 of the mode spectrum.
- 3279 • Of note, high phasic arousal has been shown to suppress multi-domain bi-
3280 ases in decision-making in humans and mice^{66–68}, including the biases toward
3281 perceptual history²⁸ that we implicate in internal mode processing. The in-
3282 crease in response speed and history congruence over time (Supplemental
3283 Section 9.4) may argue against insufficient training as an alternative expla-
3284 nation for internal mode processing, but may also taken as a sign of waning
3285 arousal. The multiple mechanistic mappings to RTs and confidence there-
3286 fore warrant more direct measures of arousal (such as pupil size^{28,65,66,68–70},
3287 motor behavior^{69,70}, or neural data⁷¹) to better delineate bimodal inference
3288 from fluctuations in global modulators of task performance.

3289 10.3.7 Comment 7

3290 In several analysis the authors present an effect and then show that this effects
3291 persists when key variables/ design aspects are also taken into account (see an
3292 example at around line 70). It makes more sense to present only one single
3293 analysis in which these key variables are controlled for. Results cannot be inter-
3294 preted if they are spurious factors driving them so it is not clear why some of the
3295 results are presented in two versions (“uncontrolled” and “controlled” analyses).

3296 We apologize for this. We have updated our manuscript accordingly and have omitted,
3297 whenever possible, reports of uncontrolled analyses (highlighted in the main text). The
3298 most significant changes are summarized here:

3299 • Group-level autocorrelation curves in humans: In line with previous work⁸, we
3300 found that the probability of stimulus-congruence was not independent
3301 across successive trials: At the group level, stimulus-congruent perceptual
3302 choices were significantly autocorrelated for up to 15 trials (Figure 2B),
3303 controlling for task difficulty and the sequence of presented stimuli (Sup-
3304 plemental Figure 2A-B). (...) In close analogy to stimulus-congruence, we
3305 found history-congruence to be significantly autocorrelated for up to 21
3306 trials (Figure 2B), while controlling for task difficulty and the sequence of
3307 presented stimuli (Supplemental Figure 2A-B).

3308 • Group-level autocorrelation curves in mice: At the group level, we found signif-
3309 icant autocorrelations in both stimulus-congruence (42 consecutive trials)
3310 and history-congruence (8 consecutive trials (Figure 3B), while controlling
3311 for the respective autocorrelation of task difficulty and external stimulation
3312 (Supplemental Figure 2C-D).

3313 • Correlation between stimulus- and history-congruence in humans: When perceptual
3314 choices were less biased toward external information, participants relied
3315 more strongly on internal information acquired from perceptual history (and
3316 vice versa, $\beta = -0.05 \pm 5.63 \times 10^{-4}$, $T(2.1 \times 10^6) = -84.21$, $p = 0$, controlling
3317 for fluctuations in general response biases; Supplemental Section 9.2).

3318 • Correlation between stimulus- and history-congruence in mice: Fluctuations in the
3319 strength of history-congruent biases had a significant effect on stimulus-
3320 congruence ($\beta_1 = -0.12 \pm 7.17 \times 10^{-4}$, $T(1.34 \times 10^6) = -168.39$, $p = 0$) beyond

3321 the effect of ongoing changes in general response biases ($\beta_2 = -0.03 \pm 6.94 \times$
3322 10^{-4} , $T(1.34 \times 10^6) = -48.14$, $p = 0$).

3323 **10.3.8 Comment 8**

3324 The central empirical finding is potentially important but is currently shadowed by more
3325 speculative sections/ discussions. For instance, the section on the adaptive merits of the
3326 computational model is relatively weaker compared to the empirical results. In particular,
3327 the model is simulated without feedback (whereas most experiments employ trial by trial
3328 feedback) and does not outperform the baseline model in accuracy but in other secondary
3329 metrics.

3330 **We agree with the Reviewer (see also a similar suggestion by Reviewer 1 in**
3331 **Comment 9). We have removed the section 5.8 and the associated subsection of**
3332 **the discussion from our manuscript. We will develop a model on the potential**
3333 **function of between-mode fluctuations in a separate publication.**

3334 **Minor comments:**

3335 **10.3.9 Comment 9**

3336 **The amount of statistical analysis and results is often overwhelming. The authors**
3337 **could streamline the presentation better such that the main result is brought to**
3338 **the foreground. Currently the manuscript resembles a technical report.**

3339 We apologize for this. From the Results, we have moved a number of sections to the Sup-
3340 plemental Materials to stream-line the manuscript (i.e., our analysis of general response
3341 biases [former section 5.4], the analysis of psychometric functions [former section 5.5], and
3342 the respective paragraphs on the IBL database). From the Discussion, we have removed the
3343 section on self-organized criticality (also following the suggestion of Reviewer 1). We have
3344 also moved more peripheral statistical results to the figure legends and the method section:

3345 • We have moved the statistics on exponential decay in the autocorrelation to the figure
3346 legends of Figure 2B and 3B.

3347 • We have shortened the description of logistic regression models that predict the stimulus-
3348 and history-congruence at the index trial from the stimulus- and history-congruence at
3349 the preceding trials.

3350 • The section on mouse behavior now matches the logic and presentation of results in the
3351 human section.

3352 We hope that these changes will increase the readability of our manuscript.

3353 **10.3.10 Comment 10**

3354 **Some typos or omissions may alter the meaning in various places. Indicatively,**
3355 **in lines 273, 439, 649.**

3356 Thanks a lot, we have corrected these typos.

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